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A STUDY OF THE VEGETATION IN THE FLORIDA EVERGLADES

CHARLES M. LOVELESS[1]
Florida Game and Fresh Water Fish Commission

INTRODUCTION

The Everglades of southern Florida comprises one of the largest freshwater marshes on the North American continent and contains the largest single body of organic soils in the world (Stephens 1956). This extensive basin began as a Pliocene sea bottom (Parker and Cooke 1944) and covers an area approximately 100 miles long by 40 miles wide. The Everglades vegetation formation itself, however, is relatively young. Carbon-14 tests have shown that the oldest peat soils in the upper Everglades area are only about 5,000 years old (Stephens 1956).

Until recently the history of this marsh has been one of unwise drainage programs, exploitation and near destruction. As an outgrowth of this the Florida Legislature enacted a plan in 1949 to execute a sound multiple purpose water conservation program in the Everglades. This plan resulted in the establishment of the Central and Southern Florida Flood Control District and provided for construction of large water retention units called Conservation Areas. In accordance with the program, the Florida Game and Fresh Water Fish Commission was given the responsibility of managing the wildlife resources of 726,000 acres in Conservation Areas 2 and 3 (Fig. 1). These two units comprise the Everglades Wildlife Management Area. In order that wildlife might be properly managed it was necessary that a study on the vegetation of the area be conducted. This paper presents some of the findings of the investigation.

The Everglades is a large freshwater marsh of very low relief whose flat physiognomy is broken only by slightly elevated sites called tree islands or bayheads. The area's principal vegetational components are the sawgrass marshes, wet prairies, slough aquatic communities and tree island communities. Surface water is usually present over the entire region for the greater portion of most years but during extensive droughts the area is almost completely dry and often swept by fire. A mantle of organic peat or muck covers most of the Everglades. These deposits are underlain with a calcareous limestone stratum of recent marine origin. Characteristic climatic features are the marked seasonal variations in rainfall, gen-

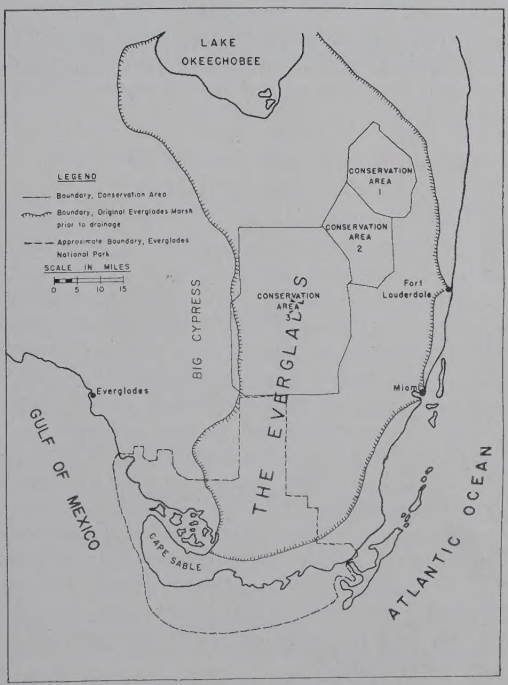

FIG. 1. Map of lower Florida showing location of Big Cypress Swamp, boundaries of Conservation Areas and Everglades National Park, and original extent of the Everglades marsh.

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erally high temperatures and humidity, and prevailing southeasterly trade winds.

Methods

A variety of field study techniques was employed in the plant community investigations. Such techniques included permanent quadrats; belt, line and association transects; and transect-sample plot clipping studies (Loveless 1957). In addition to the quantitative material collected by these methods, information was also obtained by the examination of aerial and permanent station photographs and the analysis of various observational data.

The use of permanent square meter quadrats and permanent belt and line transects in representative aquatic communities and quadrats four mil-acres in size on the tree islands proved to be effective in these areas. Repeated examinations of the plots have provided data on seasonal changes in composition as well as changes related to fire, differences in water levels and other factors. Transect-sample plot studies were also employed in both the aquatic and tree island communities. In these studies, plants were either clipped and weighed or their coverage estimated ocularly.

General information regarding Everglades vegetation and conditions prior to the intensive drainage program was obtained from local inhabitants long familiar with the area and from former publications about the region, such as those by Harshberger (1914), and Davis (1943).

Descriptions of Plant Communities

Sawgrass communities

These communities are characterized by the large sedge, sawgrass (*Mariscus jamaicensis*),[2] which comprises approximately 65 to 70 percent of the total vegetation cover of the Everglades marshes. Sawgrass is usually the dominant plant, either occurring in almost pure stands or mixed with a wide variety of other sedges, grasses, herbs, and attached emergent or floating leafed aquatic plants. The composition of such marshes is affected by prevailing water conditions. Abundance and density of plant species in the community are greatly influenced by depth of water, period of inundation, and rate of rise and fall of water levels. Sawgrass is among those species thus affected. For example, it attains greatest density on sites covered with surface water most of the year, but on relatively dry sites, occurs in thin open stands and rarely fruits.

Some sawgrass communities may be considered fire climaxes because they have burned annually during periods of drought for many years (Davis 1943). Recently, however, fires which have become more intense and widespread have reduced large areas of formerly dense sawgrass to sparse, stunted stands.

Within this general sawgrass community there are the following component community types.

Mariscus—Sagittaria—Panicum hemitomon—This community type is the most extensive association of the Everglades and covers vast areas throughout the entire marsh. Sawgrass in this type may be either sparse or dense, sometimes occurring in communities of almost pure stands. Primarily, however, it grows in association with flag (*Sagittaria lancifolia*), maidencane (*Panicum hemitomon*), pickerel weed (*Pontederia lanceolata*) and cattails (*Typha domigensis* and *T. angustifolia*). Shrubs commonly present are buttonbush (*Cephalanthus occidentalis*) and willow (*Salix amphibia*). Sufficient open water areas exist to permit the growth of such plants as *Utricularia* spp., white water-lily (*Nymphaea odorata* Ait.), floating heart (*Nymphoides aquaticum*), arrow-arum (*Peltandra virginica*), swamp-lily (*Crinum americanum*), water-pennywort (*Hydrocotyle umbellata*), *Hydrotrida caroliniana, Ludwigia natans,* water fern (*Salvinia rotundifolia*) and duckweed (*Lemna* spp.).

During drought periods a variety of incipient species invades the community and exerts seasonal dominance. Among the more conspicuous ones are pigweed (*Acnida cuspidata*), dog-fennel (*Eupatorium capillifolium*), plume-grass (*Erianthus giganteus*), beard-grasses (*Andropogon* spp.) and giant bristlegrass (*Setaria magna*). Other weed species of minor importance that are seasonally represented are the fleabanes (*Pluchea purpurascens, P. foetida* and *P. petiolata*), *Aster* spp., seashore mallow (*Kosteletzkya althaeifolia*), mist flower (*Conoclinium coelestinum*), thistles (*Cirsium* spp.) and loosestrife (*Lythrum flagellare*). Smartweeds, such as *Polygonum densiflorum, P. hydropiperoides* and *P. punctatum,* quite frequently are abundant in this community following fire, and the vines *Ipomoea sagittata* and *Funastrum clausum* are common on the stems of the larger attached emergent plants.

Mariscus—Myrica—Ilex—This type, which was probably uncommon in the Everglades prior to the initiation of drainage, has become increasingly important as a result of the general lowering of water levels and perhaps fire. It is usually confined to the drier sites and covers extensive areas in some sections (Fig. 2).

The dominant species are sawgrass and the shrubs, myrtle (*Myrica cerifera*) and dahoon holly (*Ilex cassine*). These shrubs often form

[2] Source of scientific plant names, unless otherwise indicated, is J. K. Small (1931 and 1933).

FIG. 2. A typical Mariscus-Myrica-Ilex community type in the northern Everglades.

very dense thickets which are referred to locally as "hell nests." Royal fern (*Osmunda regalis*), marsh fern (*Dryopteris Thelypteris*), and swamp fern (*Blechnum serrulatum*) are prominent members of the ground cover. Vines, such as greenbrier (*Smilax laurifolia*), *Mikania scandens,* and *Funastrum clausum* are also often abundant.

Mariscus—Panicum hemitomon—The sawgrass—maidencane type occurs irregularly over much of the region and is similar to the sawgrass—flag—maidencane type in its species components but normally occupies drier areas. It is predominantly an association of sparse to medium dense sawgrass and maidencane.

During dry years a wide variety of incipient plants such as *Bidens coronata, Aster* spp., dogfennel, plume-grass, pigweed, horseweed (*Leptilon pusillum*), mist flower, goldenrod (*Solidago fistulosa*), fleabane, meadow-grass (*Eragrostis ciliaris*), loosestrife, smartweeds, redroot (*Gyrotheca tinctoria*), and *Eupatorium serotinum* occupy this community type.

Wet prairies

The wet prairies are composed of species of *Rhynchospora, Panicum* and *Eleocharis* that form relatively low stature communities known as flats.

Rhynchospora Flats—This easily recognized and usually well defined community is one of the more typical representatives of the pre-drainage Everglades vegetation. These flats are usually covered with surface water for longer periods of time than any of the other communities, excluding the sloughs, and, except during abnormally dry years, the water level rarely recedes more than a foot below the surface of the ground.

The Rhynchospora flats are most abundant in the central and east-central portions of Conservation Area 2 and in the western and southern sections of Area 3. They frequently form transition zones between the sawgrass communities and the sloughs and generally occur as elongated strands paralleling the north-south oriented tree islands.

Originally these flats were probably more widespread than at present because it seems that many of them have been replaced by sawgrass. On the other hand, some of the former slough areas are now Rhynchospora flats and it may be that the present total area covered by them approaches the original extent, the difference being a shift in the site location of the communities as a result of the general lowering of water tables.

The predominant species in this wet-site community is *Rhynchospora tracyi,* but other plants frequently co-dominant with it include *Eleocharis elongata, E. cellulosa* and maidencane (Fig. 3).

FIG. 3. A typical Rhynchospora flat in the Hillsboro Lake section of Conservation Area 1. Note abrupt transition between the marsh and woody tree growth of the small circular bayhead.

Rhynchospora corniculata, which normally occurs only infrequently, may occasionally become abundant, particularly following excessively dry years. In the wetter portions of these flats white waterlily, floating heart, swamp-lily, and spider-lily (*Hymenocallis tridentata*) are abundant. Stunted, isolated stands of sawgrass often occur in both the ecotonal and the deep water areas. *Utricularia foliosa, U. pumila, U. purpurea* and *Ludwigia natans* are also common in the deep water areas. *Psilocarya nitens* and *Sacciolepis striata* occasionally occupy the shallower portions of the ecotone. Species of minor importance are *Proserpinaca palustris,* pipewort (*Eriocaulon compressum*), white-top (*Dichromena colorata*), *Cyperus haspans, Eleocharis equisitoides, Panicum paludivagum, Scirpus conferoides* Poir., water-dropwort (*Oxypolis filiformis*), *Rhynchospora globularis, R. perplexa, Aster exilis,* and *Gerardia purpurea* L.

In the western portion of the Everglades small, isolated stands of *Spartina Bakeri* are present in this community.

Panicum hemitomon Flats—Maidencane has apparently only recently become a dominant part of the Everglades flora. Although this species was undoubtedly present in the area prior to drainage, it was probably restricted to the drier sites. It is now widespread as a result of ability to withstand both widely fluctuating water levels and repeated burning. For example, although maidencane shows an affinity for dry sites, and attains its greatest densities in such areas, it is usually tolerant of high water levels. During periods of rising waters the plants grow rapidly, maintaining sparse stands in three feet or more of water for a period of nine months to a year. It propagates itself primarily by rhizomes, but also fruits abundantly during wet years following periods of drought. Its tolerance to fire is indicated by rapid sprouting within three or four days after burning.

A few species common in this community are *Eleocharis cellulosa, E. elongata,* pipewort, whitetop, redroot, swamp-lily, spider-lily, *Rhynchospora tracyi,* sparse, scattered stands of sawgrass, flag and pickerel weed, and occasionally myrtle, willow and holly. Many other incipient weed species, such as various panic grasses and herbs, are also present seasonally.

Eleocharis Flats—These areas are comprised in many instances of almost pure, dense stands of *Eleocharis cellulosa.* Generally, however, the community is an association of *Eleocharis cellulosa, E. elongata,* flag, white water-lily, pickerel weed, maidencane and floating heart. Most of the species present in the Rhynchospora flats also occur in this community. *Eleocharis cellulosa* can tolerate high water conditions due to its rapid growth and for this reason during such periods exerts dominance in the Rhynchospora flats.

Eleocharis flats are most conspicuously represented in the western edge of the Everglades in the ecotone between the open marsh and the Big Cypress Swamp (Fig. 4). In this area these flats are quite extensive, sometimes covering hundreds of acres.

FIG. 4. An extensive Eleocharis flat in the swamp-marsh ecotone of the western Everglades. Trees in background are cypress (*Taxodium distichum*).

Willow communities

Willows are much more prevalent in the Everglades today than formerly, according to local persons familiar with the history of the area. In a sense they are "fire followers," invading freshly burned areas, or where the soil has been disturbed by various machinery. They occur in practically every vegetative type in the Everglades, occupying a wide variety of sites and occurring in many different situations. Willows appear to be relatively unaffected by either fire (unless burning removes the peat substratum) or high water levels. Willows propagate themselves either by tillering or by wind blown seed and as water levels rise they put out adventitious roots from their trunks. They occur most abundantly adjacent to the peripheral levees and interior canals where they form pure stands of almost impenetrable thickets. As a result of repeated fires willows have replaced much of the original vegetation on some tree islands in the Everglades. They are now a common component around burned-out peat pockets and alligator holes. The ecotone between the wet prarie and tree island communities is often dominated by this shrub and it frequently forms pure, dense stands in the burned-out depressions in the interior of many islands.

Tree islands

These communities are perhaps the most striking botanical feature in the Everglades. As their name indicates, they consist of growths of low trees which occur on elevations slightly higher than the surrounding marsh. They occur generally throughout the entire region but are most abundant in the central part of Conservation Area 1 (Hillsboro Lake area).

Tree island communities may be circular to ovoid or strand-like in general outline. Circular tree islands (Fig. 3), in which redbay (*Tamala Borbonia*) is the most dominant tree species, are normally quite small in size, ranging from only about one-quarter acre to five or six acres in extent. They are usually two to three feet higher in elevation than the surrounding marsh. Tree island strands (Fig. 5), normally dominated by the tree shrubs wax myrtle and holly, are much larger in size, sometimes even exceeding 300 acres. An interesting feature of the tree island strands is that they frequently are oriented in a generally north-south direction, and are somewhat "tear-drop" in shape, with their blunt ends directed northward

toward the flow of water and the southern ends tapering to a distinct point. Davis (1943) has suggested that this orientation is a result of topographic features, causing a southward movement of water that, until recently, flowed almost unimpeded from the south rim of Lake Okeechobee nearly 100 miles to the extreme lower portion of the Florida peninsula. This southward movement of water would also perhaps explain why the northern ends of the tree island strands are three to four feet higher in elevation than adjacent marsh elevations, the assumption being that organic material was carried by the water against the ends of the islands. These elevated sites, on the northern portion of the strands, comprise about 5% of the total island's area. The remaining 95% is also higher in elevation than the adjacent marsh, rising from two to four inches on the edges to slightly over a foot in the approximate center.

FIG. 5. A tree island strand in the central Everglades basin. Large trees in foreground are strangler figs (*Ficus aurea*).

An explanation of why tree islands are located at the sites they now occupy and how they developed at these sites remains somewhat obscure. Robertson (1953) has reviewed in detail various theories offered by authors such as Davis (1943), Jones (1948) and Egler (1952), that attempt to explain the phenomenon and, in view of this, these postulations will be given only cursory attention here.

Davis (1943) suggests that tree islands developed from floating chunks of peat or from floating mats of aquatic vegetation that have become bound together around a nucleus of floating rootstocks. Jones' (1948) supposition envisions floating masses of sawgrass and suggests a succession from these beginnings to wax myrtle and finally bay trees and ferns. Egler (1952) suggests that a continuous swamp forest occupied the entire basin during preaboriginal time, and that fire restricted the tree islands to their present locations. Robertson postulates, referring principally to the southern Everglades, "that bayhead occurrence is related to solution features that produced local ponded areas in the surface leveled by erosion and marl deposition. In such depressions a succession of hydrophytic communities presumably built up present peat deposits and tree islands developed." He further opines that the linear orientation of tree islands "could have occurred through collapse of the limestone ceiling along channels of subterranean drainage."

All of these interpretations have credence, and under specific sets of conditions, in localized areas, may explain the formation processes of some tree island communities. For example, the formation of tree islands from layers of free floating peat may indeed explain the origin of the numerous circular bayheads in the Hillsboro Lake area of Conservation Area 1 and perhaps in other localized regions in the upper glades where the peat is 10 to 12 feet deep. It seems unlikely, however, that such a process could have been primarily responsible for the development of the numerous, large tree island strands over extensive areas of the Everglades, where the peat mantle is only a few inches thick or is nonexistent. Development of islands from floating mats of vegetation may have occurred in some instances but many islands in the western and southern sections are composed of woody peat down to the underlying rock stratum. This would seem to preclude, in these islands, development from hydrophytes. Egler's interpretation of an original swamp forest is supported by very little evidence. The implication that tree islands now occupy their present sites because they occur in drainage channels, and are thus afforded fire protection, does not apply to extensive tree island areas in the upper glades where, in some instances, little or no apparent relationship exists between tree island sites and localized drainage patterns. The relationship of tree island occurrence to solution features, as proposed by Robertson (1953), merits investigation as does the possibility that these areas occupy sites representing elevated ridges or domes in the rock floor. This latter condition has been observed on a few occasions in the main basin of the central Everglades by the writer.

It seems apparent, therefore, on the basis of the foregoing discussion, that there are many intriguing questions yet unanswered relative to tree island formation in the Everglades. Much additional field study will be required before this complex ecological problem is fully understood.

There are differences of conditions relative to the soil reaction in terms of pH in the Everglades

tree islands. One is because the Everglades occupies a very large area, covering approximately 3100 square miles, and the limestone rock strata in the southern areas is often only a few inches below the organic surface soils, whereas in the northern sector the thickness of the peat may be in excess of ten feet. These rock strata exert considerable influence on the pH of the soil in the southern part of the Everglades where they are in close proximity to the surface. For example, Gallatin and Henderson (1943) report the soil pH of the tree islands they sampled in the lower Everglades to range from 7.5 to 8.5 and conclude that it must be assumed these soil solutions are normally basic. In contrast to this, Davis (1943) states that the tree islands of the northern Everglades are acid. These differences in pH between the northern and southern Everglades tree islands may have some influence on the composition of the vegetation but there is a paucity of data supporting this.

Representative soil samples were collected from eight unburned tree islands and eight other islands that burned at least once in the past five years. The samples were analyzed by the United States Department of Agriculture Belle Glade Experiment Station (Table I).

TABLE I. Soil reaction (pH) and amount of mineral nutrients available in burned and unburned tree islands on peat

Status	Dominant Vegetation	No. of obs.	pH	Ca lbs/ac	Mg lbs/ac	P lbs/ac	K lbs/ac
Burned	Ilex-Myrica	8	5.82	2834	325	19	36
Unburned	Persea-Ilex	8	4.52	1303	243	34	56

These data suggest that burning raises the pH and causes large increases in the amount of calcium available and substantially increases the supply of magnesium. On the other hand, burning tends to decrease the amounts of both phosphorus and potassium.

Tree islands are the most distinct plant communities in the Everglades and quite similar floristically over the entire region. Their species components are quite definitive and they possess a distinct physiognomic structure. Also, the demarcation between them and adjacent communities is normally very abrupt, the transition zone frequently being no wider than a few feet (Fig. 3). However, an ecotone of more than 50 feet in width occasionally occurs between the dominant tree island vegetation and the open marsh communities. These transition zones are usually composed of pure stands of sawgrass, or this plant associated with lizard's-tail (*Saururus cernuus*), groundsel bush (*Baccharis glomeruliflora*), willow, buttonbush, elderberry, myrtle, custard apple (*Annona glabra* L.), and coco-plum (*Crysobalanus Icaco*). *Thalia geniculata,* golden-canna (*Canna flaccida*) and gama-grass (*Tripsacum dactyloides*) are also occasionally present in this ecotone community.

The tree island strand vegetation, excluding that occurring on the higher elevated sites of the northern ends, is structurally layered, with dahoon holly and myrtle the dominant woody tree species of the canopy. Florida maple (*Acer floridanum* (Chapm.) Pax.) and redbay are also often present in this stratum. Elderberry and groundsel bush are usually abundant in the lower or second stratum, but occasionally they may extend up into the overstory. Vines are also frequently encountered. These include *Smilax* spp., *Funastrum clausum* and *Mikania scandens.*

The ground cover in both the burned and unburned islands is composed principally of ferns that in many cases form a luxuriant, dense growth. In unburned tree islands the fern species are principally royal fern (*Osmunda regalis*), chain fern (*Anchistea virginica*), and *Osmunda cinnamomea.* In altered or burned islands the ground cover similarly contains royal fern, but marsh ferns (*Dryopteris Thelepteris*), *D. gongyloides,* and swamp fern (*Blechnum serrulatum*) are considerably more abundant than either chain fern or *Osmunda cinnamomea.* The wild Boston sword fern (*Nephrolepis exaltata*) is common on the unburned islands and species such as *Nephrolepis biserrata,* the brackens (*Pteris latiuscula* and *P. caudata*), and *Litobrochia tripartita, Psilotum nudum, Dryopteris patens* and leather fern (*Acrostichum daneaefolium*) are often present.

Many of these burned islands were originally true bayheads as evidenced from relics of burned-out bay tree stumps and logs occurring on some of them, and also the fact that in unburned areas the true bayhead type vegetation still predominates. In most sections, however, fire has resulted in a reversion of the apparent climax bay tree community to a holly—myrtle—elderberry fire subclimax associes. The frequency of fire required to accomplish this is unknown but it undoubtedly occurs in a very short period of time once an island is burned severely.

On the higher elevated sites of many tree island strands grow large strangler fig trees (*Ficus aurea*) and often some elderberry, southern hackberry (*Celtis mississippiensis*), Florida trema (*Trema florida*), castor bean (*Ricinus communis*), cabbage palmetto (*Sabal Palmetto*), Hibiscus *tiliaceus* L., wild-coffee (*Psychotria nervosa*), coffee-weed (*Ditremexa ligustrina*), and myrsine (*Rapanea guianensis*). Very infrequently such

species as slash pine (*Pinus caribaea*), royal-palm (*Roystonea regia*) and cypress (*Taxodium distichum*) occur on these sites. Fruit trees such as banana (*Musa sapientum*), sour orange (*Citrus aurantium*), papaya (*Carica Papaya*), guava (*Psidium Guajava*), mulberry (*Morus rubra*) and wild-lime (*Zanthoxylum fagara*) are often present. Some of these fruit trees were probably planted by the Indians when they utilized the islands as permanent village sites.

The ground cover on the drier more elevated sections of the tree islands is sometimes very sparse, but usually it is composed of medium to dense stands of *Rivina humilis, Dicliptera assurgens, Parietaria floridana,* and false-nettle (*Boehmeria cylindrica*). Occasionally water-pimpernel (*Samolus floribundus*), nightshade (*Solanum gracile* Link.) and pokeweed (*Phytolacca americana*) are also present. In addition, such vines as *Glycine Apios, Melotheria pendula* L., *Aster carolinianus, Ampelopsis arborea, Parthenocissus quinquefolia, Vicia acutifolia, Calonyction aculeatum,* and *Muscadinea* sp. frequently occur.

Slough communities

Sloughs are the narrow, drainage channels that are usually water-filled, or at least wet, most of the year. The "valleys" of these channels average only a few inches to one or two feet below the elevation of adjacent marsh areas. They are probably not so extensive as they once were as some of them have apparently been replaced by the wet prairie communities and by sawgrass and myrtle in some cases. This reduction in slough areas has been due mainly to artificial drainage.

Sloughs are easily recognized by their drainage patterns and by the characteristic plant species that compose them. White water-lily and floating heart are the dominant plants, with spatterdock (*Nuphar advena* R. Br.) present in the deeper portions (Fig. 6). *Hydrotrida caroliniana* is also a common component. Some species typical of the wet prarie communities are also present with white water-lily and floating heart in the transition zone between the slough community and other types of vegetation. Sparse, stunted sawgrass also grows in this zone. *Utricularia* spp. are abundant and probably play a major role in the formation of organic soils (Loxahatchee type of peat) in the slough communities. Water ferns and the duckweeds are also present, but usually occur only infrequently.

Another type of open water area related to slough drainage patterns is the alligator hole. Such holes occur, however, in most of the other communities and are often maintained as open water areas by large alligators. In slough areas, alligator holes are usually located near the southern end of the drainage channel where the water flow creates a depression. They may be elongated, following the general pattern of the slough channel, or ovoid to circular in outline. The vegetation of alligator holes is distinct and therefore usually well defined. Spatterdock is the dominant species, with some white water-lily and floating heart also present. Species represented in the narrow ecotone are willow, pickerel weed, flag, cattail and occasionally leather fern, smartweeds and primrose-willow.

Alligator holes in communities other than the sloughs are probably the result of solution and the burning out of deep peat accumulations. Some of these holes are nearly a half-acre in size, but many are only 50 to 100 square feet in extent, and with few exceptions retain water throughout the year. The basin of the alligator holes normally extends down to the rock stratum.

These water retention units are of considerable ecological significance to the Everglades fauna during dry years. For example, field investigation of a representative sample of alligator holes during the abnormally dry winter period of 1956 revealed an abundance of alligators, turtles, fishes and other aquatic vertebrates and invertebrates. Also, it was evident from the preponderance of trails leading to these water holes that they were being utilized extensively by such mammals as deer, otter, raccoon, oppossum and wild hogs. As a consequence of these and other observations, it is obvious that alligator holes are an essential feature of the Everglades environment, particularly during dry years when they provide apparently essential water for aquatic vertebrates, invertebrates and microorganisms important in certain food chains and other predator-prey relationships. These areas likewise provide a water requirement for a variety of mammalian species.

Fire

The importance of fire and its influence on the vegetation of the Everglades can hardly be overemphasized. There is little doubt that fire has been an extremely significant factor in determining the extent and composition of the various plant communities in the area. Robertson (1953), in referring to fire in the southern Everglades, writes that evidence strongly suggests "natural fire has been a constant factor affecting the local distribution of vegetation types through the ages, and that the arrangement of plant cover types has probably always been similar to that seen today."

It seems plausible to assume that during preaboriginal times fires were started by lightning. The fact that the present-day vegetation of the

FIG. 6. Dominant vegetation in this slough aquatic community is white water-lily (*Nymphaea odorata*) and spatterdock (*Nuphar advena*).

Everglades marsh is relatively fire tolerant is indicative that natural fires have occurred from the earliest times. That these fires were started by lightning is supported by recent observations of personnel in the Everglades National Park. Robertson (1953) states in reference to this, "With the establishment (in 1951) of two fire lookout stations overlooking large sawgrass areas in Everglades National Park it soon became evident that natural fires caused by lightning do occur frequently. Several fires were seen to start from observed lightning strikes in sawgrass and in tree islands of the Everglades." He states further, "Some of these fires were extinguished by rain which accompanied the electrical storm, but among them are also some of the major fires in the history of Everglades National Park."

With the advent of the Indians, and then white settlement accompanied by large-scale and ill-advised drainage programs, fires became progressively more frequent and of even greater intensity than previously as a result of the general lowering of water tables in the Everglades.

As mentioned previously, it is not surprising then that much of the vegetation in the Everglades is relatively fire tolerant because it has undoubtedly been exposed to periodic burning for a long period of time. Examples of this tolerance to burning by certain plant species have been discussed in previous sections and thus only some general observations will be made at this point.

It has been noted, in the upper Everglades area, that fires, which occur during "normal" hydroperiod cycles, when water levels do not recede more than four or five inches below the surface of the ground, seemingly have little effect on the dominant plant species composing the various marsh communities. In fact many plants, notably sawgrass, maidencane, flag and willow, recover very rapidly and appear to grow more vigorously than prior to burning. Permanent quadrat studies have shown that sawgrass is capable of attaining its original density prior to burning within a year or two after fire has reduced it to ground level.

During extreme drought periods, such as occurred in 1955-56, water levels may recede three or four feet below the surface of the ground in the northern Everglades. Under such conditions, fires not only consume the vegetation but they also destroy the upper, dry, compacted peat layers to a depth of three or four inches over large areas and up to a foot or more in localized situations. These types of burns have marked effects on the vegetation. For example, during the early summer of 1956 fire swept much of the northern Everglades marsh (Fig. 7). These fires completely destroyed many tree island communities by burning the peat substrate out from under the tree growth. Some of these areas are now open water ponds devoid of any type of emergent vegetation while others support sparse stands of sawgrass, water-lily, floating heart and other aquatic species.

FIG. 7. Wild fires such as this swept much of the marsh during the drought of 1955-56.

Prior to the last decade little thought was given to the delicate relationships existing in the Everglades between the flora and fauna and rainfall, wind, and sunlight and the area experienced considerable change, the most obvious being the effects of fires. In most sections of the Everglades the two inseparable factors of fire and drainage have altered the vegetation of many tree islands, changed the composition of many other plant communities, and resulted in the loss of organic soils.

SUMMARY

1. Results are reported from a study of the vegetation occurring in the upper Everglades area situated in southeastern peninsular Florida.

2. The Everglades is one of the largest freshwater marshes on the North American continent.

Its principal types of vegetation are the sawgrass, wet prairie, slough and tree island communities. Sawgrass communities, characterized by the large sedge, sawgrass, as well as flag, pickerel weed, maidencane and a wide variety of incipient plant species during dry years, cover a larger area than all the other types combined.

3. The second most common group of plants occurs in the wet prairie communities. These communities are composed of at least three principal associations: (1) Rhynchospora flats, dominated by the short beakrush (*Rhynchospora tracyi*); (2) *Eleocharis* flats, in which various spikerushes such as *Eleocharis cellulosa* and *E. elongata* predominate; and (3) maidencane flats, which support dense stands of *Panicum hemitomon*.

4. Slough communities, the next most common marsh community, occur in narrow, north-south oriented, drainage channels that are usually water-filled or at least wet most of the year. White water-lily is the most characteristic species. These communities have decreased in extent due to drainage and in many instances have been replaced by wet prairies.

5. Tree islands are the most clearly defined plant communities in the Everglades. Dominant tree species on the tree island strands include myrtle, holly, willow and redbay. Various species of ferns comprise the major portion of the ground cover. The northern end of most tree island strands is usually two to three feet higher in elevation than the adjacent marsh. On these more elevated sites grow such trees as strangler fig, elderberry, hackberry, sabal palmetto, wild orange, lime, guava, and papaya.

6. Circular tree islands or bayheads are much smaller in size than the strand islands and are dominated by the tree-shrubs redbay and holly. The ground cover is usually composed of a luxuriant growth of ferns. These sites are two to four feet higher in elevation than the surrounding marsh.

7. Much additional field study is required in order to explain why tree islands are located at sites they now occupy and how they developed at these sites. The development of these areas from floating chunks of peat seems a plausible explanation in some areas. The relationship of tree island sites to the topography of the underlying rock stratum merits consideration, however.

8. Natural fire has been a constant factor affecting the composition of the Everglades flora since early times. As a consequence of exposure to periodic burning over a long period of time it is not surprising that much of the vegetation is relatively fire tolerant.

9. During recent times fires have been more frequent and of even greater intensity than previously as a consequence of lowered water levels due to ill-conceived drainage programs. This has resulted in altering or completely destroying many tree island communities, changing the composition of other plant communities, and has resulted in the loss of organic soils.

References

Cooke, C. Wythe. 1939. Scenery of Florida. Fla. Geol. Surv. Geol. Bull. No. 17, 118 pp.

Davis, John H. 1943. The natural features of southern Florida. Fla. Geol. Surv. Biol. Bull. No. 25, 311 pp.

———. 1946. The peat deposits of Florida, their occurrence, development, and uses. Florida Geol. Surv. Geol. Bull. No. 30, 247 pp.

Egler, Frank E. 1952. Southeast saline Everglades vegetation, Florida, and its management. Vegetatio 3: 213-265.

Gallatin, M. H. and J. R. Henderson. 1943. Progress report on the soil survey of the Everglades. Proc. Soil Sci. Soc. Fla. Vol. A, pp. 95-104.

Harshberger, John W. 1914. The vegetation of south Florida. Trans. Wagner Free Inst. Sci., 7: 49-189.

Loveless, Charles M. 1957. Clipping study techniques in marsh ecology investigations. Proc. Southeastern Assoc. Games and Fish Comm. 11: 119-124.

Parker, G. G. and C. Wythe Cooke. 1944. Late Cenozoic geology of southern Florida, with a discussion of the ground water. Fla. Geol. Surv. Geol. Bull. No. 27, 119 pp.

Robertson, William B., Jr. 1953. A survey of the effects of fire in Everglades National Park. U. S. Dept. Int., Nat. Park Serv., mimeographed, 169 pp.

———. 1955. An analysis of the breeding bird populations of tropical Florida in relation to the vegetation. (Unpublished Ph.D. dissertation, Univ. of Ill.), 614 pp.

Small, John K. 1931. Ferns of Florida. Sci. Press. Lancaster, Pa. 237 pp.

———. 1933. Manual of the southeastern flora. Sci. Press. Lancaster, Pa. 1,554 pp.

Stephens, John C. 1956. Subsidence of organic soils in the Florida Everglades. Soil Sci. of Am. Proc. 20, 77-80.

A DIRECTIONAL CHANGE IN THE SUBALPINE FOREST-HEATH ECOTONE IN GARIBALDI PARK, BRITISH COLUMBIA

V. C. Brink
Division of Plant Science, The University of British Columbia, Vancouver

In the northwestern portion of Garibaldi Park, British Columbia, often called the Black Tusk meadows area, a dozen glaciers and glacierets have been retreating fairly steadily for one hundred years or more (Mathews 1951, Figs. 1 and 2). The glaciers were advancing several centuries ago and overwhelmed forest, remnants of which are found today on the newly bared soil (Taylor 1936). Evidence for recent climatic change here, as in many other parts of the world, is therefore conclusive. It is difficult to implicate specific factors of climate in glacier retreat and advance although Mathews (1948), Hubley (1956) and Harrison (1956) have recorded some significant data relative to temperature changes in the Pacific Northwest. Obviously the snow remaining at the end of each summer in the glacier catchment basins must be a prime integrant of the high mountain climate of the Pacific slope.

Post-Pleistocene changes in plant communities of the Pacific Northwest have been recorded by Hanson (1947). Despite the evident climatic shift over the last century, its expression in extant plant communities is not easy to discern. However, modest establishment of subalpine trees in heath in the Black Tusk area of Garibaldi Park appears to be attributable to the recent climatic shift, and a change in the snow pack, particularly, appears to be implicated in the vegetational change just as it is in the waning of the nearby glaciers. Although the impression is gained that the subalpine forest-heath ecotone is dynamic quite generally over the heavy snowfall area of the Coast Mountains of British Columbia, sites where the influences of the many ecological variables can be objectively examined are few. The Black Tusk area is one of the more suitable for study.

Physical Features

The study area, (Fig. 1) well within the Coast Mountain system of British Columbia and forty miles north of the City of Vancouver, is known for its large subalpine Garibaldi Lake, glacier-hung peaks, flower meadows, and Quaternary volcanism. The relief is bold; Garibaldi Peak 8787 ft, a Pleistocene volcano and the highest summit in the area, is only twelve miles from tidewater. Several other summits, including those of the granitic massif, Castle Towers, exceed 8000 ft. Mathews (1948, 1951, 1958) reported comprehensively on the geology, topography, and glaciology. The area is reached by float plane in summer or by foot from the Pacific Great Eastern Railway.

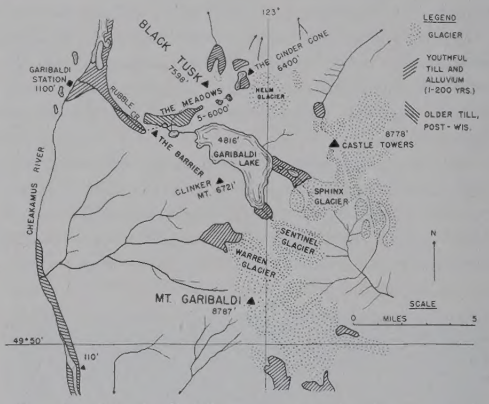


FIG. 1. The Garibaldi Lake Area showing the main glaciers and parts vacated by recession during the last century.

Climate

The climate of the Black Tusk area (Fig. 1) varies greatly with altitude, aspect, proximity to sea, and mountain mass. In the main valleys, the climate is "humid cool temperate" and supports a dense forest (climatic subdivision B of Spilsbury and Smith (1947) or Koppen type "Marine West Coast," Cfb). A meteorological station at Alta Lake, at an elevation of 2100 feet, in a main valley some forty miles from tidewater and about sixteen miles north of Black Tusk peak, recorded an annual average precipitation of fifty-five inches. Stations nearer to the sea may receive over one hundred and fifty inches of precipitation each year. More than 75% of the precipitation falls during the months from October to March. Many of the days of summer are, at all elevations, clear and dry. At 5000 feet on Black Tusk meadows, the snow pack by March commonly exceeds 12 ft; nevertheless, elevation for elevation this accumulation is less than half that on the seaward slopes of nearby Mt. Garibaldi and on the mountains 35 miles to the south near Vancouver, B. C.

Vegetation

The purpose of this paper will be served by a superficial description of the vegetation of the

study area. The botanical literature of the immediate and congeneric areas is very limited, viz., Hardy (1927), Perry (1928), McAvoy (1931), Schmidt (1957), Spilsbury and Smith (1947) and cannot substitute for the brief description.

The Marine West Coast Forest

Slopes and valley bottoms below 4000 feet, except for scattered rocky bluff, recent burn, and logged-over areas, are established, as previously mentioned, to "Marine West Coast Forest." Large trees of western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Douglas fir (*Pseudotsuga menziesii*), make up the principal cover. Sitka spruce (*Picea sitchensis*), and western white pine (*Pinus monticola*), are present but are not abundant. Red alder (*Alnus rubra*), broad-leaved maple (*Acer macrophyllum*), and black cottonwood (*Populus trichocarpa*), are common ruderal species on alluvial flat and lowland terrace. Lodgepole pine (*Pinus contorta*), is found on very light soil, bog, and rocky bluff.

The Lower Subalpine Forest

Mountain sides at elevations of 3500 to 5000 feet are established to subalpine forest with lovely fir (*Abies amabilis*), mountain hemlock (*Tsuga mertensiana*), and yellow cedar (*Chamaecyparis nootkatensis*), as the principal species.

The Upper Subalpine Forest and Meadow

Above the 5000 foot contour, the character of the subalpine forest changes markedly. Presumably it may still be called forest if the definition of Ording (Dahl 1956) is accepted. On the other hand, this contour might be regarded as the forest line or upper edge of continuous forest (Daubenmire 1954) for at this elevation treeless heath predominates. Nonetheless trees fifty feet high are common to 6300 feet. Above this elevation physiography and climate together limit the growth of tree species to shrub (krumholz). Dwarfed representatives of tree species however have been found as high as 8000 ft. The subalpine forest of the Black Tusk area in another way changes at 5000 ft.; about this elevation alpine fir (*Abies lasiocarpa*), becomes an important species; it is rarely present in the lower subalpine forest. In the undercover of the upper subalpine forest and along the forest margins, the shrubs, *Vaccinium membranaceum* and *Rhododendron albiflorum*, are abundant and *Pyrus sitchensis* and *Alnus sinuata* are not infrequent; *Veratrum viride, Valeriana sitchensis, Rubus pedatus, Lupinus arcticus, Arnica laevigata* are some of the prominent forbs. False heather (*Phyllodoce* spp. and *Cassiope* spp.) and *Lutkea pectinata* occur where the forest is open.

The treeless assemblages of the upper subalpine zone are numerous and are probably not unlike those of the high Arctic in the complexity of their successional relationships and in their interactions with the factors of snow cover, aspect, soil water, solifluction, and soil parent materials. In any event, the Black Tusk treeless communities require more study and their classification, which follows immediately, is regarded as limited and provisional.

Between 5000 and 6300 feet, the vegetation consists mainly of (1) heath, (2) sedge meadow and (3) forb meadow. Trees (4) in groves are common up to 6000 feet. The four components of the vegetational mosaic, in the growing season, are usually clearly delimited and may be plainly seen at considerable distances.

The heaths, *Phyllodoce empetriformis* and *P. glanduliflora, Cassiope mertensiana,* and *C. tetragona* are the principal plants over most of the alpine slope and flat and, very generally, meet the subalpine forest. *Lutkea pectinata* is a common associate of the heaths and constant minor associates are *Hieracium gracile, Valeriana sitchensis, Lupinus arcticus, Lycopodium alpinum, Erigeron salsuginosus, Deschampsia atropurpurea, Vaccinium membranaceum, Arnica laevigata,* and *Pedicularis bracteosa.*

On flats and moderate slopes, often sharply delimited from the heath, are sedge meadows in which caespitose *Carex* spp. (especially *C. nigricans, C. illota, C. pyrenaica* var. *austromontana*) and *Caltha leptosepala* are dominant. *Leptarrhena pyrolifolia* and *Ranunculus verecundus* are common and *Petasites frigida, Kalmia microphylla, Trollius laxus* and *Parnassia fimbriata* are occasional. Water does not stand over the sedge meadow in many places in the subalpine zone. However, the water table under sedge is high, even in mid-summer.

On many south facing slopes from 10 to 30 degrees is a community designated for the purposes of this paper as "forb meadow." Lewis (1917) in the Canadian Rockies termed similar meadow "mat-grassland"; the communities are popularly referred to as "flower meadow" because of the prominence in summer of the bright flowers of the herbaceous perennials. In early summer, the flowers of *Erythronium parviflorum, Claytonia lanceolata,* and *Pulsatilla occidentalis* are much in evidence. Later the flowers and foliage greens of many species make a spectacular display; some of the contributors to the display are *Valeriana sitchensis, Lupinus arcticus, Castilleja miniata, Os-*

morrhiza occidentalis, Arnica latifolia, Erigeron salsuginosus var. *media, Penstemon procerus, Veronica wormskjoldii, Potentilla flabellifolia, Agoseris carnea, Potentilla diversiloba, Aquilegia formosa,* and *Cirsium hookerianum.* The grasses, *Poa alpina, Phleum alpinum, Bromus marginatus, Melica smithii* and *Danthonia intermedia* and the sedge, *Carex spectabilis,* are generally present and are prominent after frost has withered the foliage of the broad leaved perennials.

The Communities of the Alpine Zone and the Primitive Surfaces

Less than 5% of the study area is at an elevation greater than 6500 feet and most of this area is made up of concordant ridges and glacier-hung summits. Dark lichens make up the largest plant community and are solidly established over stable talus, shallow soil, and rock face which, in general, is wind-swept free of snow much of the winter. *Cornicularia tenuissima* and *Umbilicaria vellea,* black lichens, and yellow lichen, *Rhizocarpon geographicum,* are the principal species.

On a few high wind-swept ridges, which may not have been glaciated, such as those named Polemonium, Gentian, and Empetrum, communities of low shrub, grasses, sedges, forbs, and lichens occur. In some locations a sod several inches thick has formed but in others the community is confined to the interstices of the angular flag. Common species are *Empetrum nigrum, Arctostaphylos uva-ursi, Juniperus sibirica, Salix* spp., *Sibbaldia procumbens, Poa alpina, Festuca ovina, Trisetum sesquiflorum, Carex phaeocephala, Carex engelmannii, Luzula spicata, Saxifraga bronchialis, Silene acaulis, Antennaria alpina, Penstemon Tolmiei, Aplopappus lyallii, Potentilla villosa,* and *Selaginella watsoni.*

Krumholz, confined to areas with a true soil, is found in solid banks on the rims of many south facing ridges at 6000 to 7300 feet. Alpine fir is the principal species but occasionally juniper, mountain hemlock, and whitebark pine (*Pinus albicaulis*) occur. Individuals of the tree species, only an inch or two in height, and some thirty-five species of grass and forbs have been collected above 8000 feet in pockets of soil along with summit-limited species such as *Poa lettermani.*

An appreciable part of the land surface above 4800 feet is devoid of vegetation or is beginning to establish a vegetative cover. The primitive surfaces, it may be pointed out, are of several kinds and their vegetation and devegetation are not within the scope of this paper. There are small solifluction areas possibly underlain by permafrost and outwash soils of special character at the Cinder Cone. Soils over which the snow lies late in certain summers, scree, talus, and the "summer-bare" surfaces of rock between the black lichen communities and nêvé are primitive surfaces of a kind (Fig. 2). Moraine, bare rock, and recent alluvium left or forming as the glaciers shrink also constitute an area of noteworthy magnitude (Fig. 1).

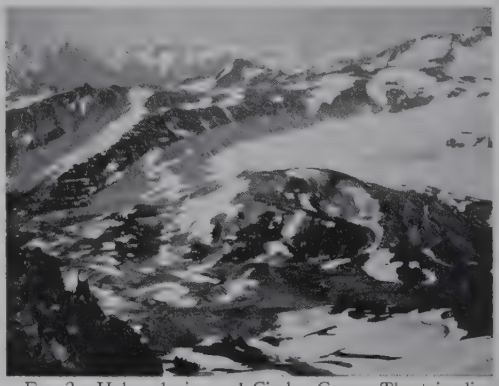


FIG. 2. Helm glacier and Cinder Cone. The trim line is 400 feet above the glacier front.

OBSERVATIONS AT THE SUBALPINE FOREST-HEATH ECOTONE

"Short" trees are establishing in heath adjoining the upper subalpine forest and grove. The establishment, although not spectacular, is apparently indicative of a dynamic ecotone. The tree species, primarily alpine fir and secondarily mountain hemlock, have established in locations where trees have not been growing before or at least not for several centuries.

The short trees are not uniformly young, or seedling, trees (Figs. 3 and 4). Until the trees exceed in height the maximum snow depth of twelve to fourteen feet, growth is limited and the correlations of age, height and trunk diameter are very low. Most ring counts were made on transverse sections, 30 microns thick, obtained with a sliding microtone; heart decay and occasional obscurities introduced appreciable error in the counts. Ring counts from large trees were obtained from increment borings and sawn cross sections. Belt transects were laid over the forest-heath ecotone and representative data are given in Tables I and II. Most small trees are younger than 100 years and most established 20 to 40 years ago. Very young fir are difficult to find in the heather but, nonetheless, it is certain that very few established in the last decade, a period, on the whole, of late snow years. Resemblances are strong to data recorded by Hustich (1949) and Mikola (1952) for Scandinavia.

TABLE I. Data from a representative belt transect "B," 28 m. × 2 m., between two patriarchal trees; elevation 5560′

		Distance in Meters																			
Blocks		0–2		2–4		4–6		6–8		8–10		10–12		12–14		14–16		16–18		18–20	
Number of trees	P* (1)	6		14		3		0		7		7		13		4		0		2	
Average age years		91.8		29.3		32.6		0		28.5		35		27		25.2		0		42.5	
Average diameter		4.25		.75		.93				.93		.72		.35		.45				.75	
Average annual increment mm		4.6		2.6		2.8				3.3		2.1		1.3		1.8				1.8	

Blocks		18–20		20–22		22–24		24–26		26–28											
Number of trees	P (1)	15		5		3		13													Total 92
Average age years		37.2		49		68		72.6													
Average diameter		1.25		3.4		3.7		4.6													
Average annual increment mm		3.3		6.9		5.4		6.3													

*P=patriarchial trees

FIG. 3. Black Tusk meadows showing, in the foreground, heath with alpine fir establishing in it, and, in the background, south-facing forb meadow.

FIG. 4. Black Tusk meadows showing small trees in heath between the forest and the Sedge-Caltha community.

The short trees are establishing in heath where, in all likelihood, trees have not grown for several centuries and maybe not in post-Pleistocene time. The soil mantle very uniformly displays a heath profile with about 6% carbon in the top 2 inches and 4.5 per cent carbon in the next 4 inches. Only in a few places are decaying roots, stump hummocks or forest soil profiles observed. Furthermore from observations on soils left by glacier recession it can be confidently stated that centuries are required to produce an organic soil profile such as that under the heath which the small trees are invading.

TABLE II. Data from belt transect "B" by age classes

Age Classes Years	Number	Age Classes Years	Number
0–10	0	61– 70	6
11–20	5	71– 80	5
21–30	34	81– 90	2
31–40	19	91–100	5
41–50	7	100–400+	2
51–60	9		

The change in the ecotone is not always easy to see. In the first place many of the mountains in the Pacific slope of the Coast Range have very limited subalpine areas and, although tree invasions of heath may well have occurred, the scale is small and "expected reproduction" and "new establishment" are difficult to separate. The elevations in the Black Tusk area on the other hand are about right for a demonstration of the ecotone dynamics. In the second place the western Coast Range mountains have been scoured by Pleistocene and Recent ice and little soil remains over the highlands. There are than strong edaphic limitations to subalpine forest extension nearly everywhere. However, in the Black Tusk area the soil mantle is fairly extensive. Therefore in this area roughly climal establishments of the short trees are to be seen: younger and shorter trees are found as distance away from the subalpine forest or grove margins increases and as the late snow areas are approached. Lastly it is to be noted that growth in the subalpine zone is very slow when compared with that of lower elevations. For example, new soils left by the retreating local glaciers over one hundred years ago have acquired a very limited cover. Development of a vegetative cover is by no means as rapid as that described by Cooper (1931), Heusser (1956) and Crocker and Dickson (1957) on the recessional

moraines of south-eastern Alaska. It is not surprising then to find little change along the ecotones in the uppermost parts of the subalpine zone. The lowermost subalpine heath is, on the other hand, well established to short trees. Few points on the heaths in the Garibaldi Lake area are more than three hundred meters from forest edge or grove but on the largest, small trees are growing at maximum "seed throw."

Establishment of small trees occurs almost exclusively in the *Phyllodoce-Cassiope* heath; virtually none occurs on the forb meadow where the soils are more xeric, and have a higher pH, and where more mineral soil is exposed, or on the sedge–*Caltha* meadow where the water table is higher and the pH is lower. An observation of possible importance, too, is that the oldest trees of the groves near and in the forb meadow are younger (though still several centuries old) and straighter than the patriarchs of the groves in the heath which are often very old and broken-topped.

The first white visitors to the Garibaldi Lake area came in the second decade of this century. Accordingly the photographic record of vegetational change is not extensive. Nonetheless photos in the possession of R. Howard and W. H. Mathews (Mathews, personal comm.) show an increase in tree height along several ecotones and two observers who have known the Black Tusk meadows for forty years state that vistas they knew in earlier days are now closed by the increasing forest. Comparison of interval photos of subalpine groves do not, however, reveal any marked increase in diameter by layering.

The Alpine Fir and Mountain Hemlock in the western Coast range are part of the snow-field vegetation. Snow depth maxima of twelve to thirty feet are common over the subalpine zone and the forest line in general bears some relationship to this. On mountains nearer the sea where snowfall is heavy the forest line may be as low as 4500 feet whereas on more distant terrain of comparable latitude and exposure, where the snowfall is lighter, as in the Black Tusk area, the forest line may be as high as 6300 feet. Indeed on some high dry mountains of the interior slope of the Coast range the forest line may be 7000 feet. Skiers and others note the later disappearance of snow from the seaward slopes, altitude for altitude. Snowfall, obviously not the sole determinant of the forest line in our study area, appears to be an important one. An observation of greater importance relates to the earlier disappearance of snow in late spring from grove and short tree areas than from the adjacent heath (Fig. 5). Although certain forb meadow communities may be free of snow first in spring, and indeed a few steep faces and wind blown ridges may not accumulate snow, very generally the subalpine trees establish on areas early free of snow—small eminences on the general surface, vale margins, etc. Special influences associated with the taller trees, such as local warming and wind cirques in the snow cover, are not necessarily involved for, in many areas, where the snow leaves early the nearest mature trees are several hundred yards distant and the small trees may be only a few inches high and unable to greatly influence the local climate.

FIG. 5. Alpine fir established on areas which first become free of snow.

Ecotones other than the subalpine forest-heath ecotone doubtless have responded to climatic change but the record is not so plainly written. The migration of pioneer species such as lupine, eriogynea, and valerian from long established heath communities into late snow areas, and landslip areas initiated by heavy snows, and into moraine and outwash below glacier and nêvé is much in evidence; lichen successions below glacier and nêvé trimlines are readily seen. However changes in extant communities are very generally dissembled; amabilis fir may be moving into alpine fir forest; red heather (*Phyllodoce*), commoner in the mid subalpine, may be displacing white heather (*Cassiope*) which is dominant at higher elevations. Certainly the latter species are dying or are in poor condition along their lower ranges.

Discussion

Griggs (1934) and Marr (1948) have recorded a recent advance of forest into tundra in the Alaskan and Canadian Arctic. However, Griggs (1938) found alpine timberlines in the western United States and adjacent Canada to be essentially static; apparent advances of forest into alpine and subalpine meadow at a number of Cordilleran locations were, he believed, related to grazing by domestic stock or to fire. The site he studied on Mt. Rainier, Washington, is, however,

the only one which may be reasonably compared to the Garibaldi Park location of this study in that both are in the high snowfall zone of the west coast mountains. The Garibaldi area was, however, well north of the Wisconsin ice front.

It seems reasonable to term the establishment of short trees in the subalpine heath a "directional" change in the sense that Churchill and Hanson (1958) use the term. The invasion of heath long established on soils left by Wisconsin ice has been proceeding for a century. It is true that change is not spectacular for the subalpine growth of the Garibaldi area is slower than that of many other areas. Then, too, the subalpine communities "accommodate," as others do, to considerable climatic fluctuation and lengthy lag periods may exist at the ecotone.

It seems reasonable that the directional change described is a reflection of climatic change for the nearby glaciers have undergone accelerated loss of volume for a century or more. At least until they grow above the snow depth maximum alpine fir and mountain hemlock, it is observed, belong to the snowfield flora. The observations of Shaw (1909), Taylor (1922), and Butters (1932), in the Cordillera give support to this view. Although snow cover is probably not a simple expression, as Griggs (1938) notes, the duration and/or depth of the snow pack over the Garibaldi meadows must have been reduced over the century. It should be noted that, in the B.C. Coast Range subalpine zone, summer is well on its way before the snow leaves the meadows and the growing season begins. Therefore the long days in which the meadows are snow free, gained in July and August, must be doubly significant in plant growth.

It appears that the advance of the subalpine trees is not a simple extension along a single front. Small trees are not establishing on the xeric south-facing forb meadows despite the presence on the meadow margins of large beautifully shaped seed trees.

The change in forest-heath ecotone in Garibaldi Park cannot be related to grazing by domestic stock, very probably not to fire, or to a gradually receding permafrost. It can be confidently stated that pack horses, the only domestic stock, have not visited most of the area and there is no reason to believe that the few native herbivores are a serious consideration. Furthermore the plants of the heath have low forage ratings. Fire is rare in the Garibaldi Lake area. Very few old trees carry fire scars and in only one pit of dozens dug was charcoal found. Fuel values in the timberline area are generally low but are highest in the dense patriarchal groves on the low scattered ridges and tree "islands." If fire was an agent in the creation of the subalpine heaths, why were the trees of high fuel value not burned? It is doubtful if aboriginal peoples would fire the meadows of the Black Tusk area for most of their food plants, such as the Indian potato (*Claytonia lanceolata*) are much more abundant to the eastward. Although permafrost occurs locally at the Cinder Cone in the Black Tusk area it has not been found elsewhere; its presence in a high snowfall area would be anomalous. Therefore a more favorable edaphic condition, attributable to waning permafrost, is unlikely. The forest-heath ecotone in the Black Tusk meadows and in the heavy snowfall area of the Coast range generally, is a dynamic one and the best explanation of change lies in the diminishing snow cover.

References

Butters, F. K. 1932. Flora of the Glacier district. Can. Alpine Jour. **21**: 139-147.

Churchill, E. D. and H. C. Hanson. 1958. The concept of climax in the arctic and alpine vegetation. Bot. Rev. **24**: 127-191.

Cooper, W. S. 1931. A third expedition to Glacier bay. Ecology **12**: 61-95.

Crocker, R. L. and B. A. Dickson. 1957. Soil development on the recessional moraines of the Herbert and Mendenhall glaciers, south-eastern Alaska. J. Ecology **45**: 169-185.

Dahl, E. 1956. Rondane. I Kommisjon Hos H. Aschehoug and Co. (W. Nygaard), Oslo. 374 pp.

Daubenmire, R. 1954. Alpine timberlines in the Americas and their interpretation. Butler Univ. Bot. Studies **11**: 119-136.

Griggs, R. F. 1934. The edge of the forest in Alaska and the reasons for its position. Ecology 15: 80-96.

———. 1938. Timberlines in the northern Rocky Mountains. Ecology **19**: 548-564.

Hansen, H. P. 1947. Postglacial forest succession, climate, and chronology in the Pacific Northwest. Trans. Amer. Phil. Soc. **37**: 1-30.

Hardy, E. A. 1927. Report on a collecting trip to Garibaldi Park, B. C. B. C. Prov. Museum Rpt. 1927, Victoria, B. C.

Harrison, A. E. 1956a. Glacial activity in the western United States. Jour. Glaciology **2**: 666-668.

———. 1956b. Fluctuation of the Nisqually glacier, Mount Rainier, Washington, since 1750. Jour. Glaciology **2**: 675-683.

Heusser, C. J. 1956. Postglacial environments in the Canadian Rocky Mountains. Ecological Monog. **26**: 263-302.

Hubley, R. C. 1956. Glaciers of the Washington Cascade and Olympic mountains. Jour. Glaciology **2**: 669-674.

Hustich, J. 1949. On the correlation between growth and the recent climatic fluctuation. Geogr. Ann. **31**: 99-105.

Lewis, F. J. 1917. Vegetative distribution in the Rocky Mountain Parks. Canad. Alpine J. **8**: 87-95.

Marr, J. W. 1948. Ecology of the forest-tundra eco-

tone on the east coast of Hudson Bay. Ecological Monog. **18**: 117-144.

McAvoy, B. 1931. Ecological surveys of the Bella Coola region. Bot. Gaz. **92**: 141-171.

Mathews, W. H. 1948. Geology of the Mount Garibaldi map area, southwestern British Columbia. Ph.D. Thesis. Univ. of Calif.

———. 1951. Historic and prehistoric fluctuations of alpine glaciers in the Mount Garibaldi map area, southwestern British Columbia. Jour. Geol. **59**: 357-380.

———. 1958. Geology of the Mount Garibaldi Map Area, Southwestern British Columbia, Canada. Bull. Geol. Soc. Am. **69**: 161-178, 174-198.

Mikola, P. 1952. The effect of recent climatic variations on forest growth in Finland. Fennia **75**: 69-76.

Perry, F. 1928. Ecological notes on the plant life of the Garibaldi Park region of British Columbia. Museum Notes **3**: 7-12. Vancouver.

Schmidt, R. L. 1957. The silvics and plant geography of the genus *Abies*. Tech. Pub. T. 46. Dept. of Lands and Forests, Victoria, B. C.

Shaw, C. H. 1909. The causes of timberline in mountains: the role of snow. Plant World **12**: 169-181.

Spilsbury, R. H. and D. S. Smith. 1947. Forest site types of the Pacific Northwest. Dept. of Lands and Forests, Victoria, B. C.

Taylor, W. P 1922. A distributional and ecological study of Mount Rainier, Washington. Ecology **3**: 214-236.

Taylor, W. 1936. Glacier retreat in Garibaldi Park. Canad. Alpine Jour. **24**: 103-108.

———. 1938. Glacier retreat in Garibaldi Park. Canad. Alpine Jour. **25**: 117-127.

AN APPARENT FROST HUMMOCK–SORTED POLYGON CYCLE IN THE ALPINE TUNDRA OF WYOMING[1]

W. D. Billings and H. A. Mooney
Department of Botany, Duke University, Durham, North Carolina

Introduction

In a recent paper, Bliss (1956) has described frost-formed peat hummocks and sorted polygons ("frost boils") in an alpine valley in Wyoming. In the course of further work in the same location, the present authors have observed what apparently is a cyclic relationship between the hummocks and the polygons which seems worthy of description.

The work was done in the Medicine Bow Mountains of southern Wyoming. The specific location is a wet meadow in a cwm on the southeast side of Medicine Bow Peak (Lat. 41° 21′ N, Long. 106° 19′ W). The floor of the cwm has an elevation of about 11,000 feet. The col at its head is at about 11,200 feet elevation, while the glacially cut cliff on the west side of the little valley rises to 12,000 feet.

The area shows abundant evidence of present and past intense soil frost action. The bottom of the valley is marked with active frost hummocks of peat, and sorted polygons surround the meltwater ponds. The slopes show some terracing due to solifluction. In the col are some very old and inactive, but large, sorted stone polygons and on top of the ridge so the west are well-developed sorted stone nets. These are above the probable level of Pleistocene ice in the cwm.

Bliss has described the sorted polygons in some detail. His diagrams and analyses indicate that the centers of the frost boils are light-colored silts and sands without plant cover, while the soil of the borders is rocky and relatively dark with organic matter. These frost boils appear to fit Washburn's (1956) descriptions of certain types of "sorted polygons," but actually may be intermediate between these and his "sorted nets." The borders are occupied by *Geum turbinatum*,[2] *Carex scopulorum, C. drummondiana, Polygonum viviparum,* and dwarf *Salix* spp. Bliss measured frost retreat in the sedge-covered peat mounds nearby, but made no attempt to correlate the various cryopedological features of the valley, this being beyond the scope of his work.

The Apparent Cycle

During the summer of 1957, observation indicated that while intact frost hummocks in peat (Fig. 2A) showed no superficial resemblance to the sorted polygons (Fig. 2E), there were many degraded and scarred hummocks in various stages of disintegration. In fact, there was no sharp line between the remnants of some badly eroded and subsequently frost-churned hummocks and certain of the sorted polygons. It was possible to find almost every type of intergradation between the hummock and the frost boil.

Cross-sections of intact and scarred hummocks were dug and the profiles plotted on cross-section paper. Several sorted polygons under different

[1] Field work upon which this paper is based was supported by the National Science Foundation under Grant G3832, Environmental Biology. Sincere appreciation is expressed for this assistance.

[2] All nomenclature is that of Harrington (1954).

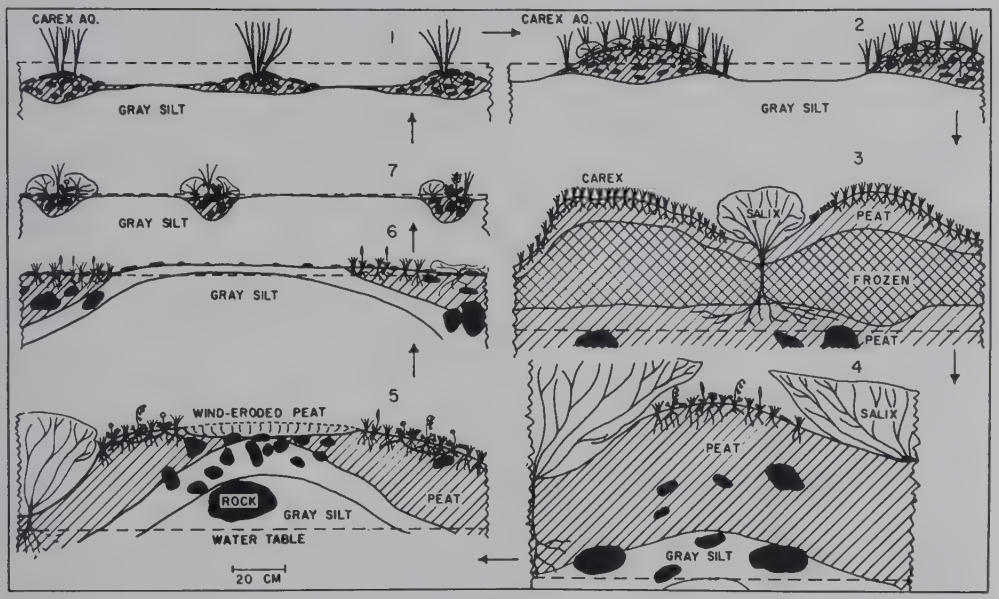


FIG. 1. The initiation of peat hummocks by vegetation and frost action (Stages 1, 2, 3, 4) in an alpine meadow of the Medicine Bow Range and the subsequent disintegration of the hummocks into frost scars (Stage 5) and sorted polygons (Stages 6, 7). Cross-sections traced from field sketches.

water-table conditions were also sectioned. All profiles are illustrated in Figure 1.

With these data in hand, it appears likely that the sorted polygons are the result of the degradation of the frost hummocks of peat. When a hummock rises high enough so that it protrudes above the snow during certain periods of strong winds (probably in the late autumn or early winter), the turf at the crest is blasted and eroded away by snow or ice particles (Fig. 2B). Repeated exposures of this type kill the plants on the crest and the peat underneath is gradually eroded away. It is difficult to say how long this takes in terms of years.

With the overburden of peat being reduced, frost thrusting from below pushes rocks and silt up above the water table and eventually out through the scar at the top of the mound (Fig. 2C). Eventually the sod (which by now has changed from *Carex* to *Geum turbinatum, Polygonum viviparum,* and other "climax" species) dies back some distance from the scar, the peat disintegrates, and the hummock is base-leveled, with the rocks and a little peat now surrounding the scar as a border (Fig. 2D). The degraded hummock is now essentially a sorted polygon (Fig. 2E) with the water table not far under the surface. Stages 5 to 7, inclusive, in Figure 1 illustrate this degradation part of the cycle. They were traced directly from field drawings.

The building-up stage of the cycle is not so easily seen and there are gaps in our field data concerning some of the stages. Further field work, it is hoped, will fill these gaps. Stages 1, 2, 3, and 4 in Figure 1 depict the building up of peat mounds from frost boil borders.

The surface of an ordinary frost boil during much of the summer is only a few centimeters above the water table. The center of the boil is slightly higher than the rocky borders. But the quaking water-saturated silt[3] is almost like quicksand and any weight will cause the center to become depressed until it is below the water table. During dry years such as 1954 and 1955, the water table in late summer may be 20 cm. or more below the surface. In years of heavy snows, such as 1957, however, the water table may rise until it is one or two decimeters *over* the frost boils. When this occurs, all of the plants on the rocky intervals are killed, the peat washed away, and the rocks exposed (Fig. 2F). The bottoms of many meltwater ponds consist of these drowned sorted polygons which may be just as active as those above the water table.

A fluctuating water table which occasionally drowns the boils may speed up the formation of

[3] Our analysis by the Bouyoucos (1936) method shows: sands 42.3%, clays 11.9%, and silt 45.8%. An analysis by Bliss (1956) from the same area indicates sands 44%, clays 8.9%, and silt 47.1%.

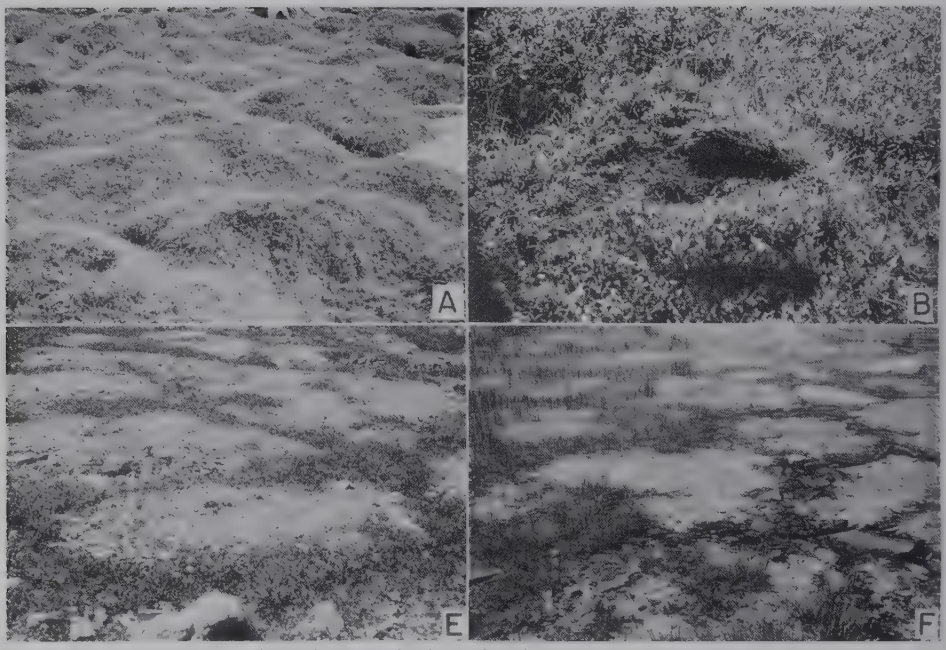
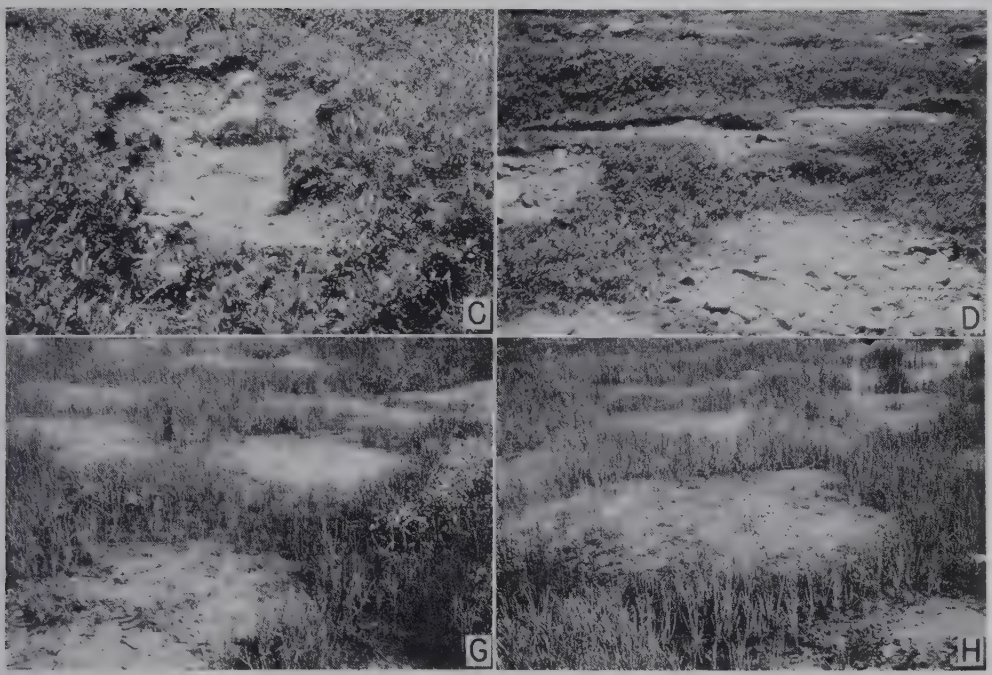


FIG. 2. Photographs of the major steps in the cycle. A. Peat hummocks covered with *Carex drummondiana* with *Salix brachycarpa* in the depressed intervals. B. Start of a frost scar caused by wind-erosion at the crest of a peat hummock. C. Older frost scar with rocks and silt being thrust through peat from below. D. Extensive degradation of peat hummocks into young sorted polygons. E. Mature sorted polygons. F.

new frost hummocks by allowing excellent growth of one or more species of *Carex*. The pioneer plant on drowned polygons is *Carex aquatilis* which invades the rocky intervals in several centimeters of water as shown in Stage 1, Fig. 1 and Fig. 2F. Peat mounds form slowly in the *Carex aquatilis* sod and eventually get above the water table (Fig. 2G and H). On these embryonic hummocks, *Sedum rhodanthum, Salix* spp., and mosses form an understory to the larger *Carex* as shown in Stage 2. It may be possible that peat mounds do not have to originate on drowned frost boils but form also on the intervals of boils where the water table is just at the surface, as in Stage 7. The intervals of such polygons do have some *Carex aquatilis,* but here it is mixed with *Salix anglorum* var. *antiplasta, Pedicularis groenlandica, Sedum rhodanthum,* and other species. These small hummocks may develop into peat mounds without being submerged. This, however, seems less likely than mounds originating in water from *Carex aquatilis*. At any rate, the water table does fluctuate and the new mounds start on the rocky intervals of frost boils, and are pioneered by *Carex aquatilis*. It is not known how long it takes to build up some 60-70 centimeters of peat in the mature mounds. But it is easy to imagine the coalescing of the embryonic mounds into a solid cover of peat over the waterlogged silt of the sorted polygons. Such an insulating layer of peat may well slow down and even stop thrusting frost action in the silt itself until the top of the peat mound begins to erode away as described earlier. The cycle is thus reinitiated.

The complete cycle on level ground probably consists of two phases (1 and 2), each of which is made up of three principal stages: frost hummock (FH), frost scar (FS), and frost boil (FB). These phases and stages are depicted diagrammatically in Figure 3. Briefly stated, a point in the center of the frost hummock stage of phase 1 will eventually be in the center of the frost boil stage at the end of that same phase. Phase 2 starts on the rocky *intervals* of phase 1, thus its hummock, scar, and frost boil centers, theoretically, will be offset the distance of an average polygon radius from the centers in phase 1. Two complete phases, therefore, are needed to complete the ideal cycle.

It would seem that a solid substratum is necessary for the intense frost action described above. This could be a bedrock base under the water-saturated silt, or perhaps, permafrost. Bliss (1956) did not find permafrost here, but his search



Drowned sorted polygons with *Carex aquatilis* initiating succession on rocky intervals. G. Young peat hummocks starting in shallow water under *Carex aquatilis* and other species in right middleground and upper right-hand corner. H. Similar to G, with crest of young hummock in lower left-hand corner.

was incidental to other things. Retzer (1956), however, has recently reported permafrost from the mountains of Colorado to the south of our research area, and it would not be surprising to find it here.

While there is a voluminous literature on soil frost phenomena in the Arctic, similar phenomena in alpine regions have received relatively scant attention. It is not the intention to review such literature in this short paper. However, in the Rocky Mountains, in addition to the previously mentioned work of Bliss (1956) and Retzer (1956), Richmond (1949) has investigated stone nets and stone stripes in the alpine areas of the Wind River Mountains of Wyoming. Gams (1941) has described peat hummocks in the Alps, and Zeuner (1949) reports miniature soil frost phenomena on Mt. Kenya, as does Goldthwait (1940) in the Presidential Range of New Hampshire. Goldthwait also describes inactive stone nets and stripes in the same range. Troll (1944), in his extensive review of "Strukturboden," lists several mountain localities where alpine soil frost patterns have been noted. There is no mention in any of these papers of a peat hummock-sorted polygon cycle.

In arctic Alaska, Hopkins and Sigafoos (1950) describe the disintegration of peat by wind erosion where the peat is shallower than the depth of the summer thaw. They clearly describe the formation of "peat rings" with centers of silt (essentially, frost boils) initiated by the breaking of the peat by expansion of the frozen silt from below. The early stages are relatively rapid and in a few years the peat ring is mature. The silt in these rings may be completely colonized by cottongrass (*Eriophorum*) or, in many marshes, the peat ring may represent the ultimate or equilibrium stage. While frost scars in rocky soils were beyond the scope of their paper, they did indicate that stone polygons may result from the enlargement of such scars. No mention is made of a cycle.

Hanson (1950), also in Alaska, describes how small peat hummocks may build up by frost action or vegetative growth and eventually become dried out and disintegrate. But he does not indicate that such disintegration results in sorted polygons.

Summary

Observations on peat hummocks, frost scars, and sorted polygons in an alpine wet meadow of the Medicine Bow Mountains, Wyoming, appear to indicate that wind-erosion and frost thrusting

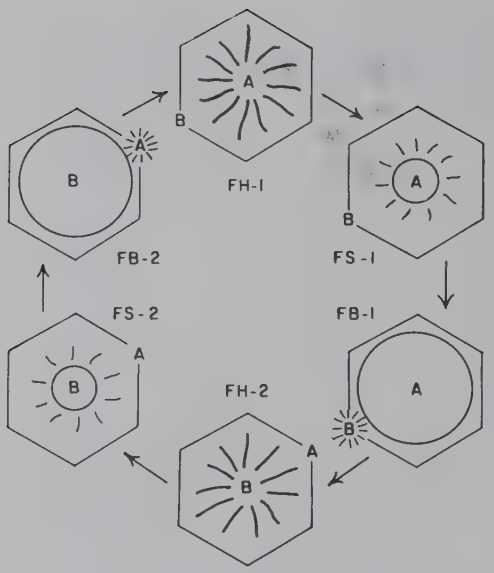


FIG. 3. Diagrammatic representation of the peat hummock-frost scar-sorted polygon cycle as viewed from above. Points A and B are fixed. Point A is in the center of the hummock in Frost Hummock 1, in the center of Frost Scar 1, and in the center of Frost Boil 1. Point B is on the interval. Assuming a new peat hummock originates at Point B due to drowning of FB 1, then Point B will be in the center of Frost Hummock 2, Frost Scar 2, and Frost Boil 2, while Point A will be on the interval. The two-phase cycle will be reinitiated again if a new peat mound originates at Point A or any other point on the interval.

can cause degradation of mature peat hummocks through frost scars to sorted polygons (frost boils). The rocks which are thrust through the scar from below form the intervals of the sorted polygons while waterlogged silt forms the centers. Subsequent drowning of the sorted polygons by a rising water table allows the invasion of *Carex aquatilis* on the rocky intervals. Small peat mounds are initiated here which may grow larger by slow accumulation of peat. Later, freezing and thawing increase the rate of expansion of the hummocks until they may be snow-free at critical times in the winter. Blasting by snow and ice particles in strong winter winds produces frost scars on the crests of the hummocks and degradation starts. Thus, it appears that these phenomena are parts of a natural cycle in which "climax" tundra on the mature mounds is really only temporary.

REFERENCES

Bliss, L. C. 1956. A comparison of plant development in micro-environments of arctic and alpine tundras. Ecological Monog. **26**: 303-337.

Bouyoucos, G. J. 1936. Directions for making mechanical analyses of soils by the hydrometer method. Soil Sci. **43**: 225-229.

Gams, H. 1941. Torfhügelmoore in den Zentralalpen. Naturwiss. Mschr. "Aus der Heimat," 54 Jg.

Goldthwait, R. P. 1940. Geology of the Presidential Range. New Hampshire Acad. Sci. Bull. **1**, 43 pp.

Hanson, H. C. 1950. Vegetation and soil profiles in some solifluction and mound areas in Alaska. Ecology **31**: 606-630.

Harrington, H. D. 1954. Manual of the plants of Colorado. Sage Books, Denver. 666 pp.

Hopkins, D. M., and R. S. Sigafoos. 1950. Frost action and vegetation patterns on Seward Peninsula, Alaska. U. S. Geol. Surv. Bull. **974-C**: 51-101.

Retzer, J. L. 1956. Alpine soils of the Rocky Mountains. Jour. Soil Sci. **7**: 22-32.

Richmond, G. M. 1949. Stone nets, stone stripes, and soil stripes in the Wind River Mountains, Wyoming. Jour. Geol. **57**: 143-153.

Troll, C. 1944. Strukturboden, Solifluktion und Frostklimate der Erde. Geologische Rundschau **34**: 545-694.

Washburn, A. L. 1956. Classification of patterned ground and review of suggested origins. Bull. Geol. Soc. Amer. **67**: 823-866.

Zeuner, F. E. 1949. Frost soils on Mt. Kenya and the relation of frost soils to aeolian deposits. Jour. Soil Sci. **1**: 20-32.

THE REGULATION OF GERMINATION IN *ORYZOPSIS MILIACEA*[1]

D. KOLLER[2] AND M. NEGBI[3]

Oryzopsis miliacea (L.) Asch. et Schw. is a perennial grass. In Israel it occurs in all regions with more than 350 mm mean annual rainfall. Several stands occur in regions with less direct rainfall, but which receive supplementary soil moisture (e.g. loessial and gravelly wadis, and waterspread areas in the Negev; cf. Tadmor and Hillel 1956 a).

Three distinct varieties of *O. miliacea* which occur in Israel and differ in morphology, habit and habitat have been described by Seligman *et al.* (1957): "grey" with silvery-grey dispersal units,

[1] This work was carried out under a grant from the Ford Foundation.

[2] Department of Botany, Hebrew University, Jerusalem, Israel. Present address: California Institute of Technology, Pasadena, Calif.

[3] Department of Botany, Hebrew University, Jerusalem, Israel.

"brown" with chocolate-brown dispersal units, and "Negev" growing in the arid Negev desert.

The species is considered very promising for pasture and has in fact been improved in the U. S. for that purpose, under the name of "Smilo."

Reseeding with *O. miliacea* (the "grey" and "brown" varieties) has been carried out in the Galilee for some time. In this region (700 mm mean annual rainfall) fall sowing results in limited emergence during the following spring, and some more during the next rainy season (Z. Naveh, personal communication). Reseeding with the same species and types was also tried in water-spread areas of the Negev, around S'deh Boker (100-150 mm mean annual rainfall), but was almost entirely without success (D. Hillel, personal communication). A similar lack of success with Smilo has been reported from Southern California (H. Hellmers, personal communication).

The dispersal units are 1-2 mm long and 1 mm thick, and each consists of a brown caryopsis enclosed in indehiscent glumes (palea and lemma).

The authors wish to express their gratitude to the Ford Foundation, which supported this work, to the Soil Conservation Service, Israeli Ministry of Agriculture, for the seed supply, and to Messers N. H. Tadmor, D. Hillel (Boguslav), Z. Naveh and A. Avraham for their cooperation in the field trials. Thanks are also due to Prof. M. Evenari for his advice and criticism.

Materials and Methods

Unless otherwise specified, the dispersal units used were harvested from "grey" and "brown" types growing at the Soil Conservation Service Nurseries at Migdal Ashkelon. This plantation was established before the various types were recognized, and the material obtained was consequently a mixture of the two types. This source is also generally used for reseeding material.

Germination was tested in Petri-dishes containing one layer of filter paper and 3 ml tap water (or other liquid, as specified). In almost all cases 100 dispersal units were sown in each Petri-dish. Daily alternating temperatures consisted of 8 hours at one temperature and 16 at another.[4]

Tests of germinability were usually carried out in the dark, but the dishes were exposed to diffuse light for 1-5 minutes at each germination count. The latter were started 3-5 days after sowing and then repeated every other day. The counted seedlings were removed.

The procedure differed in all other tests of germination responses, where both light and temperature were controlled. White fluorescent lights were installed in the incubators, giving an intensity of 100-120 fc. A "short illumination" lasted 5 minutes, and was given in the incubator.

All bio-assays of inhibitors were carried out at 20°C in the dark, with dispersal units which had been subjected to the standard acid treatment described below.

The extracts were prepared by vigorously shaking the dispersal units in water, by means of a mechanical bottle-shaker.

Germination results are given in average percentages ± deviations (in case of two replicates) or standard errors (in case of more than two replicates.[5]

The results are presented and discussed under the three major divisions which follow.

Enveloping Structures

Germinability of intact dispersal units

Tests were carried out with dispersal units which had been collected in various habitats in Israel, and it was found that some of these varied greatly in their capacity to germinate (Table I). The results indicate a line of demarcation between dispersal units originating in the more humid regions (with over 400 mm mean annual rainfall) and those originating in the arid regions (with less than 150 mm). The dispersal units from the latter regions (apparently belonging to the "Negev" variety) had a remarkably better germinability than those from the former. This phenomenon will be further discussed later. Another characteristic of the dispersal units of the "Negev" variety was that their germinability improved with time after harvest. Thus the dispersal units harvested in Nahal Nashran and Nahal Hoglot in 1954 gave 21 ± 2 and 30 ± 4 percent germination, respectively, when tested in September of the same year, and more than double that percentage when tested again in April, 1955 (Table I). The causes were not investigated.

The germinability of the nursery grown units of *O. miliacea* was tested at 20°, 26°, 30°, 10°/20°, and 20°/30°C. At constant temperatures germination was very low, occurring only at 20° and 26°C, and not exceeding 15% within 14 days. Of the alternating temperatures which were tested, only the 20°/30°C one permitted germination (about 42%).

Acid treatment

The voluminous literature on improvement of germination by sulphuric acid treatment has been

[4] In specifying the alternation, the temperature prevailing for 16 hours is written first, and separated from the other temperature by an oblique (thus 30°/20° means 16 hours of 30° alternating daily with 8 hours at 20°).

[5] Deviations and S.E. are given merely as indicators of variability between replicates and are not meant as confidence intervals for the true means.

TABLE I. Percentage of germination at 20°C of dispersal units originating in various localities in Israel (final count on 13th day). Tested: April, 1955

Locality	Annual Rainfall (mm)*	Harvested	Germination
Bayit Vagan	600 - 700	1954	0
Ein Kerem	600 - 700	1954	0.5±0.5
Eytanim	600 - 700	1954	2.0±2.0
Beth Shemesh	400 - 500	1954	0
Nahal Shorek	400 - 500	1954	0
Ashkelon	400 - 500	1953	4.5±0.5
Nahal Nashran†	100 - 150	1954	54.5±1.5
Nahal Hogloth†	100 - 150	1954	65.0±1.0

*"Climatological normals", 1952
†In small wadis

TABLE II. Effects of conditions of storage on germinability of acid treated and untreated units (1953 harvest) at 20°C (final count on 12th day). Tests were carried out 7, 15, 22, 28, 35, 42, 49, 56, 70, 155 and 326 days after treatment

	Germinability before storage	Storage conditions	Germinability throughout storage
Untreated controls	2.0±1.3	Uncontrolled	1.79±0.44
		Over $CaCl_2$	2.15±0.93
		Vacuum over $CaCl_2$	1.80±0.51
Acid treated units	94.5±0.5	Uncontrolled	72.80±5.68
		Over $CaCl_2$	86.30±1.50
		Vacuum over $CaCl_2$	91.77±1.00

reviewed in several articles (Porter 1949, Crocker and Barton 1953, Koller 1955, E. H. Toole *et al.* 1956). In most cases this treatment results in improved permeability to water of structures enclosing the embryo. *Oryzopsis hymenoides* (Stoddart and Wilkinson 1938, Toole, V. K. 1940), Smilo grass (Laude 1951) and the local *O. miliacea* (Taubman 1953) also respond to such acid treatment.

The acid treatment was carried out by shaking the dispersal units in a separatory funnel containing twice their volume 70% v/v analytical grade H_2SO_4. Shaking was stopped one minute before the end of treatment to allow the dispersal units to float to the top and facilitate draining off the acid. The funnel was rapidly filled with water, thoroughly shaken, and the contents transferred to a beaker. The supernatant was decanted, and the units washed thoroughly to remove debris and the traces of the acid.

Units thus treated for an appropriate length of time could withstand prolonged dry storage with only slight variations in germinability. The figures in Table II represent average germination percentages of a series of tests carried out at intervals over a period of 11 months with units which had been stored after treatment in open containers, over $CaCl_2$, and in vacuum over $CaCl_2$. Untreated controls were similarly stored, and each test was run in duplicate. Another set of experiments could show no significant difference between storage at 10°/15°C and 30°/36°C alternating temperatures.

Relation between the condition of units at time of acid treatment and the effectiveness of duration of treatment.—Untreated units, stored from harvest to time of treatment (thirteen months) in ordinary glass containers, and in vacuum over $CaCl_2$, respectively, were subjected to various durations of a standard acid treatment, and then germinated at 20°C. The relation between course

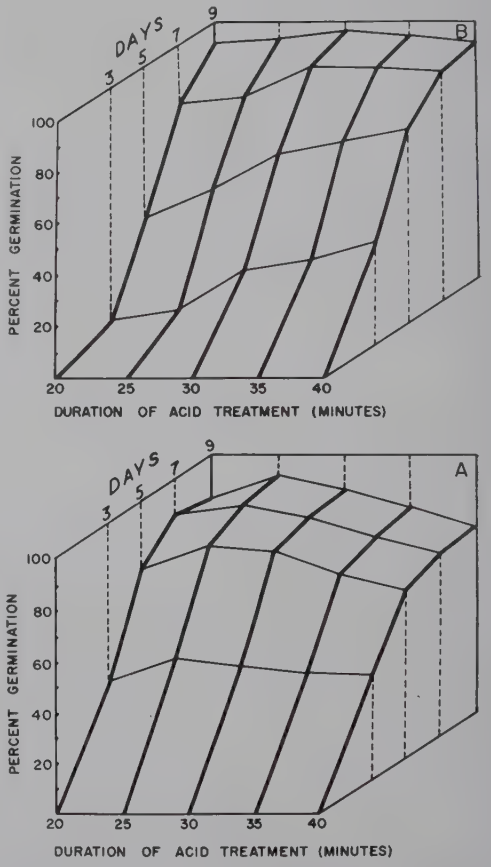


FIG. 1. Relation between the condition of the units at time of acid treatment and the effectiveness of the duration of treatment. Explanation in text. Four replicates per test.
A—storage under uncontrolled conditions
B—storage under reduced air and vapour pressure

of germination and duration of treatment is plotted in Fig. 1. These data indicate a difference in susceptibility to acid treatment between units

stored under uncontrolled conditions (A) and those stored under conditions of reduced air and water-vapor pressure (B). In uncontrolled storage the initial germination percentages are relatively unaffected by duration of treatment, but final percentages are progressively reduced with increasing duration (above 25 minutes). In dry vacuum storage, on the other hand, initial percentages increase progressively with duration, but final percentages are relatively unaffected.

A reduction in final germination percentage with increasing duration of treatment may be attributed to increasing damage to the embryo, while a rise in initial percentage with increasing duration is indicative of a progressive removal of a germination-retarding obstruction. If this assumption is correct, it seems that reduction of moisture content tends to make the germination-retarding obstruction more resistant to acid treatment, at the same time protecting the embryo from damage by the acid.

Mode of action of the acid

Water uptake.—The results of two experiments summarized in Table III show that intact units take up water at least as readily as acid treated ones, indicating that the effectiveness of the acid treatment does not result from the removal of an obstruction to water uptake by the caryopsis. A similar phenomenon was observed in other grasses (E. H. Toole *et al.*, 1956; V. K. Toole, 1939, 1941).

TABLE III. Percent water uptake* of untreated and acid treated units. Two replications of 5.0 gr each per test

	PERCENT WATER UPTAKE	
	Test I (24 hours soaking)	Test II (41 hours soaking)
Untreated Units ..	32.2±0.2	33.4±2.9
Acid treated units.	27.6±1.5	30.5±1.4

*Additional weight times 100 divided by initial weight.

The site of the inhibition.—Naked caryopses were obtained by rubbing dispersal units between sheets of emery-cloth, and selecting the undamaged caryopses under low-power magnification. Germinability tests of mechanically de-glumed caryopses, acid treated, and untreated dispersal units were carried out at 20°C (three replicates, approximately 100 units each). Mean final germination percentage (on 9th day) of acid treated units was 88.0 ± 2.5, that of the mechanically de-glumed caryopses 21.7 ± 1.0, and that of the untreated controls 2.5 ± 0.6.

These results show that removal of the glumes alone had only slightly improved germinability, in comparison with acid treatment. (The slight improvement caused by the mechanical treatment may be due to some mechanical change in the caryopsis, which occurred during treatment and remained undetected. Thus, germination of the de-glumed caryopses could be further increased by a factor of 1.5, by merely pricking them). It is therefore likely that the site of the inhibition does not lie in the glumes.

Freehand sections of untreated units, and of units subjected to an optimal acid treatment showed that acid treatment results in removal of several external layers of the caryopsis, as well as total removal of the glumes. The anatomy of the external layers of the intact caryopsis is shown in Fig. 2. Acid treatment entirely removes layers

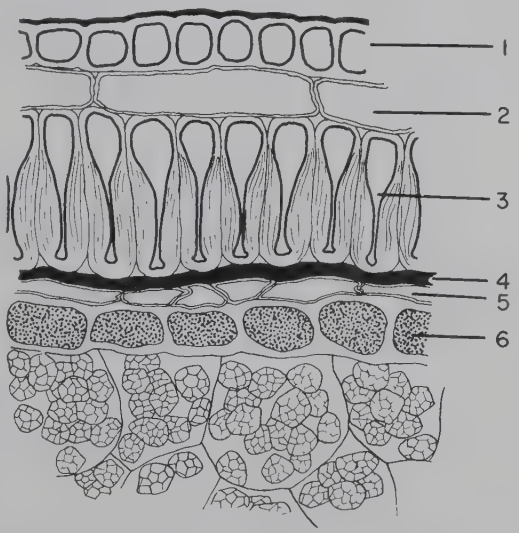


FIG. 2. Anatomy of the external layers of the caryopsis of *Oryzopsis miliacea* (see text).

1 and 2, and leaves layer 3 disorganized. The underlying layers are apparently undisturbed. By comparison with the wheat grain (Percival, 1921; Hayward, 1938) it seems that all the affected layers belong to the pericarp. It is the pericarp then which must contain the inhibitory mechanism. Weight (per 100) of acid treated, mechanically de-glumed, and intact dispersal units was found to be 68.54 ± 0.45, 83.61 ± 0.76 and 92.41 ± 0.56 mg, respectively (means and S.E. of 10 separate determinations). The inhibitory portion of the caryopsis which is removed by acid treatment amounts to nearly 18% of its weight.

The presence of inhibitors.—The results led to an investigation on the presence of inhibitors. Intact units were extracted in a tenfold amount of water (by weight), at room temperature, during 41 hours. Final (9th day) germination of acid

treated units at 20°C reached 37 ± 1% in the extract and 73 ± 5% in the water control (2 replicates per test).

To compare the inhibitor content of acid treated, mechanically de-glumed, and intact dispersal units, these were extracted for 50 hours at 26°C in twice their weight distilled water. Duplicate lots of acid treated units were germinated in the various extracts, and also in distilled water and in tap water, as controls. Final (7th day) percentages of germination are given in Table IV.

TABLE IV. Germination at 20°C of acid treated units (1953 harvest) in various media (Description in text)

Germination medium	Percent germination (on 7th day)
Tap water	95.5±2.5
Distilled water	92.5±2.5
Distilled water extract of intact units	33.0±3.0
Distilled water extract of mechanically treated units	23.0±1.0
Distilled water extract of acid treated units	89.0±1.0

In comparing the inhibitory activity of the various extracts it must be remembered that though equal weights of material were extracted, the number of units varied inversely with unit weight from the various treatments. Inhibitor content is more likely to parallel the number of units in the extracted sample. This may explain why mechanically de-glumed units exerted a stronger inhibitory activity than intact units.

The results clearly indicate the presence of inhibitors in both intact units and naked caryopses. Since disorganization of the pericarp by acid treatment results in loss of inhibitory activity, it appears that either the pericarp actually contains the inhibitor, or that it acts as a differentially permeable membrane which maintains a high concentration of the inhibitor in the caryopsis.

Ecological considerations

The relatively good germinability of the units from the arid regions could be further improved by the standard acid treatment (Fig. 3). It appears therefore that the difference in germinability between the "Negev" variety and its more humid relatives is of a quantitative nature, and is reflected in the degree of requirement for acid treatment. This may be a difference in inhibitor content, in susceptibility to the inhibitor, or in some property of the pericarp.

The higher germinability of the arid variety, relative to that of the more humid ones, may be ecologically significant. Under natural conditions the latter produce units which would germinate after prolonged exposure to moist conditions in

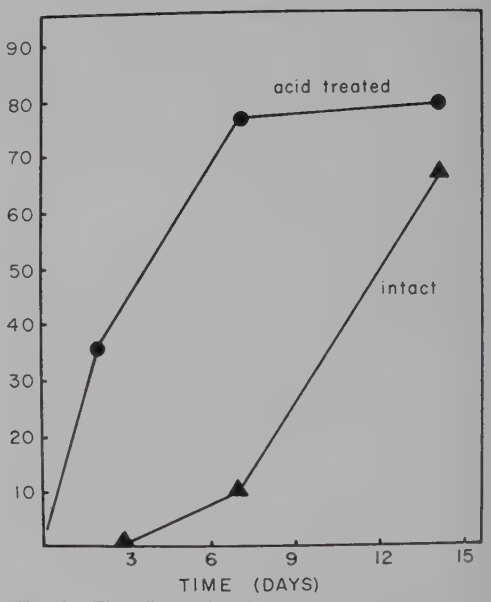


FIG. 3. The effects of acid treatment on germinability of dispersal units of the "Negev" variety (harvested in S'deh Boker, 1953). Two replicates per test.

the soil, while the former would do so after relatively shorter exposures. Such a regulatory mechanism is of marked survival value for both. The whole of Israel is semi-arid to arid, no rainfall occurring for at least 6-7 months between spring and fall. Even during the rainy season rainfall is uncertain as to amount and frequency, and this irregularity becomes more extreme from the semi-arid to the arid regions. Germination-regulatory mechanisms which would delay or prevent germination from occurring before a sufficient amount of soil moisture has accumulated for seedling establishment, are consequently of high survival value (e.g. Went, 1952; Koller, 1955). The two types of *O. miliacea* which are thus distinguishable by their germinability, show a marked adaptability to the climatic conditions of rainfall in their natural habitat. The arid variety is adjusted to scarcity of soil moisture, and its germinability is likewise geared to it, while the humid varieties are geared both in growth and germination to a more abundant and prolonged supply of soil moisture. It is likely that the qualitative aspects of this germinability are a function of the ecological conditions under which the units had matured on the mother plant (cf. Lona, 1947; Von Abrams and Hand, 1956).

Application of the results to reseeding

As a result of this work, reseeding in the Negev is now carried out either with properly treated

units from the ecotypes raised in the humid north, or with untreated units of the "Negev" ecotype (Tadmor and Hillel, 1956 b). Experimental reseeding in the Judaean Hills[6] also showed the effectivity of using treated units. Thus, for example, reseeding at a depth of 2 cm in Terra Rossa soil in the winter of 1955/56 gave 3% emergence with untreated units, and 31% with acid treated units.

Light and Temperature

The germinability tests described above followed a standard routine: counts of germinated seeds were made at intervals throughout the test period, and the seedlings removed at the time. This routine exposed the units to inconstancies in environment, the most obvious of which were: changes in the number of seedlings growing in the same enclosed space, repeated aerations and short illuminations (of dark-germinating units). In critical experiments on the effects of light and dark the germination dishes would remain unaired, sometimes in constant darkness, and with increasing numbers of seedlings. The results of the preliminary experiments dealing with the above factors (Table V) showed that, at 20°C, there was a certain percentage of acid treated units which were capable of germinating in total darkness. The germination of these is apparently completed within four days. The remaining units were evidently made to germinate by the short illuminations which they had received on the 4th and 6th days. The continuous presence of the germinated seeds in the dishes did not affect germination in the light, and only slight effects were obtained on dark germination by airing the dishes (in the dark) for 5 minutes on the 4th and 6th days.

Effects of a short illumination on dark germination

The results described above indicated that germination of acid treated units at 20°C is inhibited by constant dark, and that this inhibition is overcome by short illuminations.

Subsequent experiments were run with a single short illumination to determine the relationship between time of application of this illumination and its effectiveness in promoting germination. This effectiveness was found to be equal at 24, 48 and 72 hours (Fig. 4). Since similar results were obtained in dishes which were unopened throughout the 8-day long test as in those dishes which were opened for 5 minutes every 24 hours, it seems that aeration in the dishes was adequate.

Further tests showed that the percentage of dark-germinating units and the light-sensitivity of the remaining (dark-inhibited) units was maintained unchanged throughout a prolonged imbibition in the dark (Table VI).

The sensitivity of acid treated units of *O. miliacea* to a single short illumination is therefore much more stable than in photoblastic lettuce "seeds," where the ability of the imbibed seed to respond to a short illumination is lost fairly

[6] Carried out by Mr. A. Avraham of the Israeli Ministry of Agriculture, in cooperation with the authors.

Table V. The effects of short illuminations on germination of acid treated units at 20°C in the dark. Illuminated dishes received a short illumination once on the 4th and again on the 6th day. Two replicates per test

Light treatment	Other treatment	Percent Germination On 4th day	6th day	8th day
Short illuminations	Seedlings removed at time of illumination	40.5±1.5	84.0±3.0	96.0±1.0
	Seedlings not removed	43.0±2.0	90.0±2.0	94.5±1.5
Constant darkness	Dishes aired	—	—	49.0±3.0
	Dishes unaired	—	—	42.0±0.0

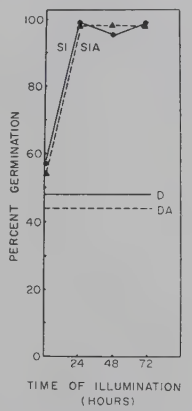


Fig. 4. The effects of aeration, and of a single short illumination on 8th day germination percentages of acid treated units (EK 1954 harvest) at 20°C in the dark. Two replications per test. D = Constant dark; SI = Short illumination; A = aerated.

Table VI. The effects on dark germination (of acid treated units) of a single short illumination when applied after various periods of imbibition in the dark. Duplicate lots per test, germinated at 20°C

Pre-illumination period of dark-imbibition (days)	% germination at time of illumination	Post-illumination germination (% after a further 7 days in darkness)
6	38.5± 0.5	91.5±1.5
14	37.0± 4.0	96.5±1.5
21	39.5± 0.5	93.0±4.0
28	39.5±11.0	95.0±2.0

rapidly (Evenari and Neumann, 1953). A similar high stability was demonstrated in *Amaranthus retroflexus* (Kadman-Zahavy, 1957, unpublished data).

The saturating short illumination varied in duration in material from different sources and harvests, but these variations were slight.

The effects of drying on the products of the short illumination were investigated. Four equal portions of acid treated units (1955 harvest) were imbibed at 20°C in the dark. After 24 hours two of the portions were subjected to a short illumination. One of these was then immediately dried over granulated $CaCl_2$ at 20°C in the dark, for 24 hours, and then resown. The other illuminated portion was returned to darkness without further treatment. Of the two remaining portions, one was dried as described above and then resown and the other was left untouched. The whole treatment of the unilluminated units was carried out in total darkness at 20°C. Four replicates were used per treatment, and were counted eight days after the initial sowing. The ratio of germination after the short illumination to that in constant darkness was 2.64 in the dried units and 2.63 in the undried ones. Likewise, the ratio of germination of undried to that of dried units was 1.05 in constant darkness and 1.05 after a short illumination. The slight excess in undried over dried units in both cases is easily explained when one considers that dried units had one day less for germination (the dessication period) than the undried units. It is thus clear that interrupting the process of germination on the 24th hour by a 24 hour period of drying has no effect on final percentages, and furthermore that the effects of the short illumination are irreversible by drying. A similar behavior has been demonstrated in other light sensitive species, such as tobacco (Kincaid, 1935).

Interaction between light and constant temperatures

The effects of constant darkness, constant light, and of darkness interrupted at various times by a single short illumination were studied. One experiment was run at 20°C and 30°C, respectively, and another was run at 26°C (with dispersal units from a different source). The short illumination was applied once per treatment, at a different time in each. All dishes were aerated for 5 minutes every 24 hours, without changing the light and temperature regime of the treatment. Whenever aeration coincided with illumination the two were given simultaneously. Counts were made 8 days after sowing.

The results in Fig. 5 clearly show the following

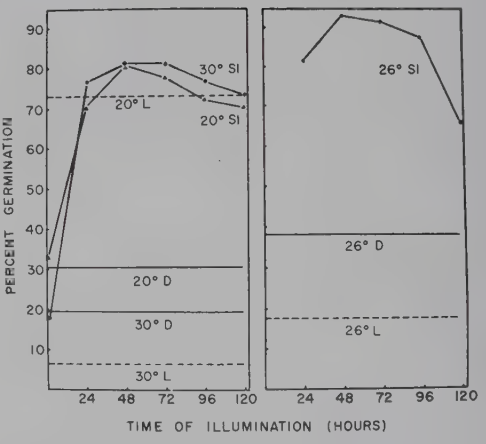


FIG. 5. The effects of a single short illumination on dark germination of acid-treated units (1953 harvest) at 20° and 30°C and at 26°C. Two replications per test. Explanation in text. L = Constant light; D = Constant dark; SI = short illumination.

facts: (a) Constant darkness was inhibitory to germination at all temperatures. (b) At the two higher temperatures (26° and 30°C) constant light was even more inhibitory to germination than constant darkness. At the lower temperature (20°C) the effect of constant light was opposite, providing a marked stimulation over constant dark. (c) A short illumination given at any time between 24 and 120 hours was highly stimulatory to germination, irrespective of germination temperature, and whether constant light had a promotive or inhibitory effect at that temperature: there was hardly any difference between the results after a short illumination at the two extreme temperatures (20°C and 30°C; cf. Fig. 5).

(At first glance it seems that the sensitivity to a short illumination reaches a maximal value on the 48th hour and gradually declines thereafter. It must, however, be remembered that no such decline was observed in long-term experiments with a short illumination (Table VI). In the present experiment all treatments were counted simultaneously, allowing progressively less time for the manifestation of the effects of the later short illuminations. This decline after the 48th hour is therefore only apparent and in actuality sensitivity is maintained thereafter at a more or less constant level.)

These results indicate that in the germination of acid treated units of *O. miliacea* three distinct, but probably interrelated processes are operative: (a) a process carried out in constant light, the quantitative effects of which are highly dependent on temperature; (b) a process carried out in

constant darkness, which is inhibitory to germination at all temperatures tested. The dark process is also temperature dependent. No simultaneous comparison was made between germination at the three temperatures, but comparisons between two temperatures always showed that the higher the temperature the higher the dark-inhibition (e.g. $20° = 51 \pm 1\%$ vs. $26° = 38 \pm 1\%$; $26° = 31 \pm 0\%$ vs. $30° = 19.5 \pm 1.5\%$). (c) A process carried out by a short illumination, which completely reverses the dark process. This process seems to be independent of temperature, within the range tested.

Of late, reports have been accumulating of "photoperiodic" effects on germination of some seeds (Toda and Isikawa, 1951; Isikawa, 1954; Isikawa and Shimogawara, 1954; Black and Wareing, 1955; Vaartaja, 1956; Stearns and Olson, 1958). The processes described above become significant in this respect when one considers their similarity to those in photoperiodic induction, as analyzed by Naylor (1953) and Bonner and Liverman (1953). In photoperiodic induction there is also a "high intensity light process" which is apparently temperature-dependent (e.g. Parker and Borthwick, 1939; Mann, 1940), and a "dark process" which, besides being temperature dependent (Hamner and Bonner, 1938; Long, 1939; Parker and Borthwick, 1939; Lang and Melchers, 1943), is completely inhibited by a "low intensity light process" (Hamner and Bonner, 1938). The latter is apparently independent of temperature within the physiological range (Biebel, 1942; Harder *et al.*, 1944). The similarity between the low intensity light process in germination and photoperiodic induction of flowering has already been stressed (E. H. Toole *et al.*, 1956). There is also a striking resemblance between the germination behavior of *O. miliacea* and the flowering behavior of the short-day-plant *Kalanchoë blossfeldiana,* where constant dark, as well as constant light, are inhibitory, while a light flash of one second duration every 24 hours is sufficient to initiate flowering (Harder and Gümmer, 1947). There would thus seem to be some common basis for photoperiodic induction of flowering and of germination, as proposed by the various workers, but whether the various processes described above have more than accidental basic similarity to those in photoperiodic behavior remains to be seen.

The effect of temperature alternations

Previous experiments had shown that the best germination of intact (non-acid-treated) units of *O. miliacea* was obtained at a temperature alternation of 20°/30°C. This is a common phenomenon in several species, particularly grasses (Harrington, 1923; Morinaga, 1926) and has been discussed (Went, 1958; E. H. Toole *et al.*, 1955 a & b). The same response to daily alternating temperatures was also observed in acid-treated units of *O. miliacea* (Table VII): A 20°/30°C

TABLE VII. Germination (% on 8th day) of acid treated units (1953 harvest) at 20°, 30° and 20°/30°C in constant light and dark and after a short illumination on 48th hour. Two replicates per test

	Constant Light	Constant Dark	Darkness interrupted by a short illumination
20°C.....	73.0±2.0	30.5±1.5	80.5±1.5
30°C.....	6.5±0.5	19.5±2.5	81.0±2.0
20°/30°C.....	64.5±0.5	63.0±4.0	81.0±0.5

daily alternation stimulated germination in both constant light and constant dark (except at 20°C, where light is not inhibitory to germination). This alternation seems to eliminate any difference between the processes carried out in constant light and those carried out in constant dark (cf. also Fig. 6). Analogously, the processes carried out by a short illumination seem to eliminate the differences between the various temperature regimes (constant and alternating). It may be said that when the temperature is alternating, a level of germination is achieved which is unaffected by constant light or constant dark. Similarly, a short illumination results in a level of germination which is unaffected by the temperature of germination. This seems to be the case also in *Nicotiana tabacum* var. Maryland Mammoth and Kentucky, and in *Brassica juncea* var. Chinese Broadleaf (E. H. Toole *et al.*, 1955 b). The processes caused by the short illumination may even be synergistic with those caused by the temperature alternations, as seems to be the case with *Lepidium* seeds (E. H. Toole *et al.*, 1955 a). It therefore seems that the short illumination process is not directly related to the alternating temperature process, though both are stimulatory to germination.

As with germination at constant temperatures, it was found that even under the favorable 20°/30°C alternation, time did not affect the sensitivity of the acid treated units to a short illumination. A single short illumination, applied at any time between 24 and 120 hours from sowing, was equally effective in increasing germination over controls in constant light or dark at 20°/30°C alternation (Fig. 6).

More work was done on the time relationships and other effects of a temperature alternation on germination in darkness of acid treated units.

Germination was started off at 20° and 30°C, respectively. Some treatments involved a single 8-hour period at the higher or lower temperature, given at different times ("single thermoperiod"). Other treatments involved a single transfer from the initial temperature to the higher or lower one, at various times ("unilateral transfer"). One treatment at 20°C involved three separate 8-hour periods at 30°C ("multiple thermoperiod"). Constant temperature controls were run at 20° and 30°C. The various thermoperiods and unilateral transfers were applied on the 48th, 96th and 144th hours, respectively. No light was given throughout the test period, which lasted 10 days in all. The results (Table VIII) may be summarized as follows:

TABLE VIII. The effects of thermoperiod, and of a unilateral temperature change on dark germination of acid-treated units (1955 harvest). Two replicates per test

Temperature treatment	Time of Change (hours from sowing)		
	48	96	144
Unilateral transfer series.			
20°⟶30°	9.0±1.0	34.5±4.5	32.0±0.0
30°⟶20°	27.5±4.5	10.5±1.5	7.5±0.5
Singe thermoperiod series:			
20°⟶30° (8 hours)⟶20°	54.0±7.0	53.0±5.0	50.5±5.5
30°⟶20° (8 hours)⟶30°	9.0±0.0	3.5±0.5	0
Multiple thermoperiod:	⟵ 67.0±0 ⟶		
Constant temperature series:			
20° Constant	⟵ 32.0±4.0 ⟶		
30° Constant	⟵ 0.5±0.5 ⟶		

(a) Unilateral transfers which were made after the 48th hour failed to adjust germination percentages from those at the initial temperature to those at the final temperature. The change evoked in germination (increase or decrease in percentage) by the unilateral transfer would thus seem to be most prominent when the transfer is made during the preliminary stages of germination (at least up to the 48th hour). It appears therefore, that the "thermal determination" of germination is not made during that initial period. In other words, it is only the temperature existing during the latter part of the germination process, which determines the final percentage of germination. This also seems to be the case with *Betula pubescens* (Black and Wareing, 1955).

(b) Germination at 20°C is equally improved by a single 8-hour thermoperiod at 30°C applied on the 48th, 96th and 144th hours. The multiple thermoperiod (8 hours at 30° on the 48th, 96th and 144th hours) was more effective in promoting germination than any single thermoperiod.

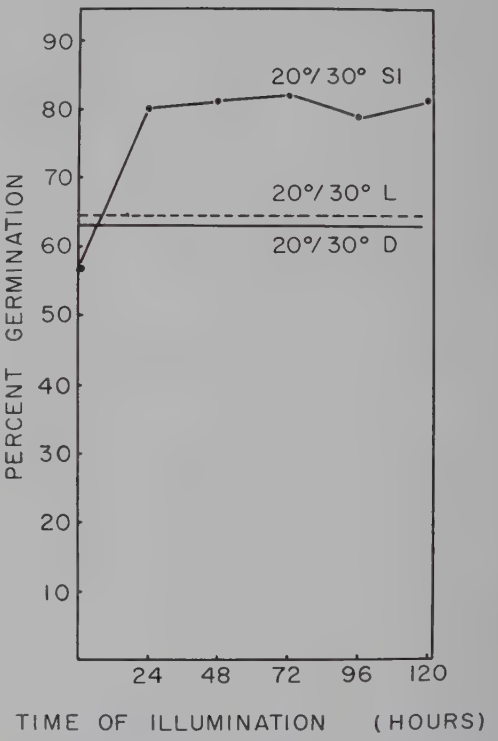


FIG. 6. The effects of a single short illumination on dark germination at 20°/30°C daily temperature alternation. Three replications per test. Legend as in Fig. 5.

This behavior is in marked contrast to the unilateral 20°→30°C transfer. The unilateral transfer does not raise percentage above that of the 20°C controls, whereas the thermoperiod invariably does so. It would appear that the unilateral transfer does no more than adjust germination to the temperature prevailing, provided it is made before the onset of the period of thermal determination. The above mentioned thermoperiod would then seem to work independently of the thermal determination mechanism: First, it actually stimulates germination over any of the controls, and secondly, it does so even when applied during the period of thermal determination where a more prolonged stay at 30°C is non-promotive.

In contrast to the single 30°C thermoperiod at 20°, the single 20° thermoperiod at 30° shows only very slight stimulation over the 30°C constant, and is always less than the unilateral 30°→20°C transfer. There thus seems to be a basic difference between the two thermoperiod treatments. The effect of the 20° thermoperiod seems to be identical with the thermal determina-

tion: The same percentages are obtained at 30°C by applying 20°C during the first 48 hours, as by giving only 8 hours of 20°C starting with the 48th hour. The information to date is as yet insufficient to formulate a general hypothesis regarding the mode of action of a diurnal thermoperiod in germination (Harrington, 1923; Morinaga, 1926; Went, 1948, 1953; Koller, 1954; Toole et al., 1955 a & b, 1956), though some have been suggested for lettuce (Cohen, 1958). The only thing that can be said is that such a thermoperiod sometimes has profound effects on germination, particularly in light-sensitive seeds.

Changes in response to light and temperature

Most of the work reported above was done on dispersal units harvested in 1953. These gave very uniform results up to the middle of 1955. Tests in the latter half of 1956 showed that some of the responses of these units had changed, particularly with regard to the temperature dependence of the processes carried out in constant light and constant dark (Table IX, a). Dark germination had increased at both 20°C and 30°C, and the inhibition by constant light at 26°C had disappeared. The processes caused by the short illumination are apparently unchanged.

TABLE IX. Changes in germination response to light and temperature, of acid-treated units. Two replicates per test. (Results rounded off.) L—constant light; D—constant dark; SI—darkness interrupted on 24th hour by a single short illumination

Testing date	Duration of test (days)	20°C			26°C		
		L	D	SI	L	D	SI
(a) *Units of 1953 harvest*							
Nov. 19, 1954	8	90	51	85	18	38	93
May 28, 1956	5	78	66	85	86	46	76
(b) *Units of 1955 harvest*							
May 30, 1956	5	3	17	29	3	6	20
June 5, 1956	8	5	16	60	..	..	.
July 1, 1956	8	..	21	55	.	.	..
Nov. 16, 1956	8	31	32	68	.	.	..

Experiments carried out in 1956, with units harvested in 1955, showed that though these units also responded to a short illumination, their germination under all conditions was relatively low (Table IX, b). However, percentages at 20°C seem to be in the process of increasing with time of storage, more so for germination in constant light than in constant dark.

Detailed experiments on the relation between age of the units and their response to light and temperature conditions were not carried out. However, from the data which could be gleaned from the numerous tests, as exemplified in Table IX, the following observations may be made.

Regulation of germination by constant conditions of temperature and illumination is gradually reduced with age. The restrictions which are relaxed earliest are those at lower temperatures (e.g. 20°C) and only later at higher ones (e.g. 26°C). (It will be remembered that as late as November, 1954, germination of 1953 harvested units at 26°C is very low in both light and dark). Secondly, it is clear that the restrictions caused by constant light undergo a more rapid decay than do those causing inhibition by constant dark. The gradual relaxation with age of temperature limits for germination is a well known, though yet unexplained phenomenon.

The effects of a short illumination on intact (non-acid-treated) dispersal units

Experiments on the effects of a short illumination on germination of intact dispersal units could be fruitfully carried out only with the "Negev" variety, since the other varieties had an inherently low germinability as a result of their inhibitor content.

Dispersal units harvested in El Migra were used, and the results (Table X) showed that the same sensitivity to light exists in intact dispersal units as in acid-treated ones. As acid treatment improves germinability of the "Negev" variety in the same manner as of the more humid varieties, it may be concluded that light sensitivity in acid treated dispersal units is not a result of acid-treatment, but that its existence in intact units is normally masked by the powerful germination inhibitor they contain.

TABLE X. Germination of intact dispersal units of the "Negev" variety (El Migra, 1953) at 20°C, as affected by various conditions of illumination. Four replicates (50 units each) per treatment

	Germination percent on 7th day
Constant darkness	36.5±2.1
Darkness interrupted by a short illumination* on 24th hour	61.5±1.5
Darkness interrupted by a short illumination* on 48th hour	64.5±2.6
Constant light	19.0±1.0

*10 minutes duration

INHIBITORS

The results reported under "Enveloping Structures" have shown that the beneficial effects of the sulphuric acid treatment were due to removal of a water-soluble germination inhibitor. The following deals with some of the properties

of the inhibitor in intact (non-acid-treated) dispersal units.

Leaching effects

The water-solubility of the germination inhibitor in intact dispersal units of *O. miliacea* has suggested that germination of this species may be rain-dependent, as is the case in other arid zone species (Went, 1952; Soriano, 1953; Koller, 1955). This possibility was further investigated with simulated rainfall.

Intact dispersal units (1953 harvest) were loosely wrapped in glass wool and inserted into vertical glass tubes. Water from a faucet was dripped through the tubes at a slow, uniform rate. Treatments of different durations (24, 48, 72 and 93 hours, respectively) were started at intervals so as to end simultaneously. At the same time, other units were soaked in water for the same periods. At the end of treatment, two replicates (50 units each) from each treatment were sown. The remaining treated units were air-dried for 24 hours and two replicates were then sown under the same conditions.

Germination of the soak-treated units was not improved at all in comparison with untreated controls, reaching no more than 6% within 15 days from sowing. The simulated rainfall treatment, on the other hand, improved germination, indicating the rain-dependence of the germination. Progress of germination of undried drip-treated units is plotted in Fig. 7, with the origin of the Time axis coinciding with the start of treatment.

Simulated rainfall of longer duration (72 and 93 hours) was more effective than one of shorter duration (24 and 48 hours), indicating a progressive leaching of the inhibitor to some threshold value. That the greater effectiveness of the longer treatments is due merely to the fact that they afforded a longer germination period (i.e. that units from the prolonged treatments germinated sooner merely because they had more time to do it in) may be ruled out. This may be readily seen from Fig. 7, where progress of germination is plotted from the first contact of the units with water, and from Fig. 8, which shows that germination of dried drip-treated units remained practically unaffected by the intervention of the 24-hour drying period. This indicated that it is the presence of a water-soluble inhibitor in the dispersal unit of this species which makes its germination rain-dependent.

The fact remains, however, that even the best drip-treatment was still less effective than the acid treatment in promoting germination. Whereas the latter makes it possible for some 80-95% of the units to germinate within 8-10 days, the former

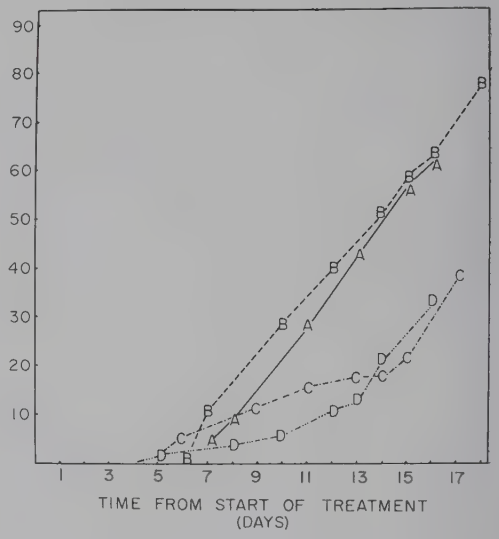


Fig. 7. Progress of germination (at 20°C) of undried drip-treated units, as affected by duration of treatment. Origin of Time axis coincides with start of drip-treatment.

Legend

Symbol	Duration of treatment
A	93 hours
B	72 hours
C	48 hours
D	24 hours

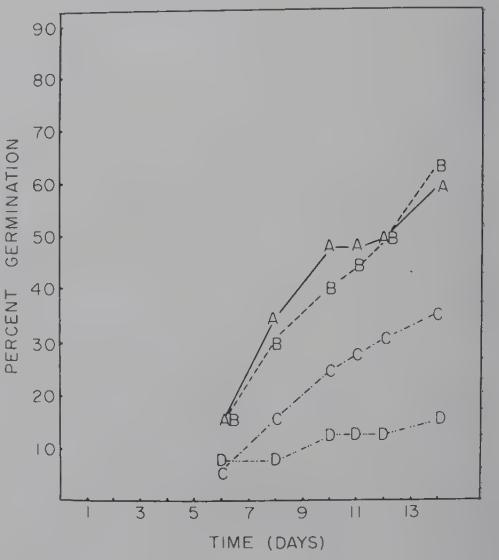


Fig. 8. Progress of germination (at 20°C) of dried drip-treated units, as affected by duration of treatment. Origin of Time axis coincides with time of sowing. (Legend as in Fig. 7).

enables only 30-35% to germinate in the same period, and only 60-70% within 14 days. This retardation could result from imperfect leaching, or from mechanical hindrance by the intact pericarp and glumes to the protrusion of the embryo.

Some properties of water-extracts from intact dispersal units

The following properties of the extract were investigated, with regard to its effect on germination and growth of the seedlings: (a) pH, (b) osmotic value, (c) stability to heat, (d) the effects of dialysis. In assessing the results it must be borne in mind that germination of the acid treated dispersal units which were used in the bioassay is inhibited by darkness at 20°C, that practically all dark germination at that temperature is completed within 4 days, and that the inhibition by darkness may be reversed by a single short illumination given at any time after the first day (see Table V).

One hundred gr of untreated units were extracted in 200 ml tap water for 6 hours, and the extract was divided into three equal parts. One of these was used directly, another was heated to the boiling point, and the third was dialyzed against running water for 40 hours through a collodion membrane. Half the dialyzed extract was heated to the boiling point. The pH and osmotic values of the various extracts were determined (the latter cryoscopically, according to Walter, 1931). Two replicates of acid treated units were sown in each of these extracts. A count of dark-germination was made on the 4th day, the remaining units received a short illumination and were returned to darkness until the final count on the 8th day, when all seedlings were weighed. The results are summarized in Table XI.

TABLE XI. Properties of the inhibitory water-extract from intact dispersal units (1953 harvest). Germination tested at 20°C in the dark, with acid treated dispersal units. Details in text

Medium	Germination Percentage		Seedling weight (8th day) in mg	Osmotic value (atm)	pH
	4th day	8th day			
Tap water	54	80	5.4	—	—
Original extract	14	50	4.4	2.41	6.77
Boiled extract	16	63	1.8	2.35	6.80
Dialyzed extract	48	65	4.8	0.36	6.52
Boiled dialyzed extract	46	80	3.9	0.12	6.35

The effects of the various extracts on germination percentage in darkness (at the 1st count, after 4 days in darkness) and after a short illumination (at the last count, 4 days after the short illumination) have to be dealt with separately. Considering first the germination in darkness, it appears that the inhibitory effects of the extract are maintained after boiling, but are greatly reduced by dialysis. This indicated that the substance inhibitory to germination is heat stable and of small molecular weight.

Germination percentages after the short illumination do not differ markedly in the various extracts. However, the inhibitory action of the original extract is evident, and there are indications that boiling or dialysis reduce this activity. When both are applied together, the reduction is complete.

As regards seedling weight, the results are unexpected. Seedling weight was reduced only slightly in the original extract, the dialyzed one, and the dialyzed-boiled one, but was very low in the boiled extract. Taking seedling weight as a measure of growth, it would seem that the germination inhibitor in the original extract has no effects on growth, and that some growth inhibitor is activated by boiling.

The osmotic value of the original extract is too low to account entirely for the inhibitory effects of the extract on germination (cf. Fig. 9), and does not appear to be changed by boiling, though it was lowered by dialysis. The pH values of all the extracts were very nearly equal (6.35-6.80). These observations indicate that neither osmotic effects nor pH play any major role in the inhibitory effects of the extracts (Evenari, 1949).

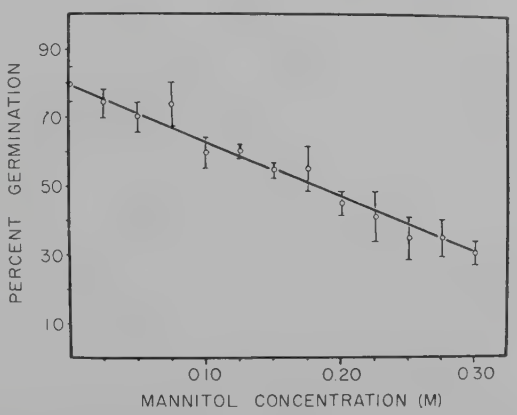


FIG. 9. The effects of Mannitol concentration on germinability (percentages on 8th day) of acid-treated units at 20°C (Means and S.D. of four replicates).

In another experiment, intact units were extracted for 6.5 hours in 1.5 times their weight of water. Some of the extract was dialyzed against running water during 25 hours and another portion was boiled for 3 minutes. The extraction and dialysis were carried out at 23.5-24.0°C, and the flasks with the original and boiled extracts were

TABLE XII. The effects of the inhibitory water-extract from intact dispersal units on germination and seedling growth at 20°C in the dark, before and after a short illumination. Explanation in text

	Germination Medium											
	Water			Original extract			Dialyzed extract			Boiled extract		
	Mean	Standard Deviation	Standard Error	Mean	Standard Deviation	Standard Error	Mean	Standard Deviation	Standard Error	Mean	Standard Deviation	Standard Error
Germination percentage												
on 4th day*	*53.5*	4.2	1.9	*24.4*	4.3	1.9	*44.2*	8.6	3.8	*24.4*	1.8	0.8
on 8th day†	*87.5*	3.1	1.2	*58.6*	1.6	0.7	*80.2*	2.5	1.1	*74.8*	1.5	0.7
Seedling weight (mg)												
on 4th day*	*1.353*	0.184	0.082	*1.243*	0.108	0.048	*1.503*	0.072	0.032	*1.087*	0.031	0.01
on 8th day†	*4.770*	0.596	0.231	*3.299*	0.414	0.186	*3.602*	0.386	0.173	*1.541*	0.407	0.182
Ungerminated unit weight (mg)												
on 4th day	*0.871*	0.048	0.021	*0.905*	0.029	0.013	*0.908*	0.029	0.013	*0.899*	0.076	0.035

*Uninterrupted dark.
†Darkness interrupted by a single short illumination on 4th day.

kept at the same temperature. Ten replications of germination tests were made with each extract at 20°C in the dark. After 4 days, 5 dishes were removed from each treatment, the seedlings counted and weighed, and the ungerminated units weighed separately. The remaining dishes were exposed to a single short illumination and returned to darkness for 4 more days. Seedling counts and weights were then carried out. Weight per seedling, or ungerminated unit, was then calculated for each dish. Mean germination percentages, seedling weights, and ungerminated unit weight, for the various treatments and germination media are given in Table XII.

These results may be summarized as follows: (a) After 4 days in the dark, both the original extract and the boiled one inhibited germination to the same extent. Dialysis removed some, but not all, of the inhibitory activity.

After a 5 minute exposure to light, followed by 4 more days in the dark, the percentage of germination increased in all the extracts and in the water controls. However, the percentages in the original extract were still the lowest, while in the boiled and in the dialyzed extracts they approached those of the controls. This increase is particularly prominent in the boiled extract, where percentages have increased more than in all others. At a given temperature, a certain proportion of the population of dispersal units is capable of germinating without a light stimulus (dark-germinators). Of the rest, a certain proportion may be stimulated to germinate by a short illumination. The fact that an almost equal additional germination was obtained by light in water (+ 34%), original extract (+ 34%), and dialyzed extract (+ 36%), may indicate that the unboiled inhibitor acts only on the dark-germinating fraction of the population, but this requires confirmation.

At 20°C, dark germination in water is completed within the first 4 days, and any additional germination in water in the subsequent 4 day period may therefore be attributed to the short illumination. The question arose whether the increase in germination in the extracts during the subsequent 4 day period was also due to the short illumination, or to the fact that the inhibitory extract merely delays germination. This aspect was therefore investigated and the following results obtained.

(b) The weight of ungerminated units after 4 days in the dark was very nearly equal in all media. The differences were not significant at either 1% or 5% level. This supports the contention that osmotic effects may be ruled out.

(c) After 4 days in darkness seedling weight varied in the following order: dialyzed extract > water > original extract > boiled extract. The latter is significantly lower than the other three ($P < 0.01$).

After exposure to a short illumination and 4 more days growth in darkness there was a large increase in seedling weight in all media, except the boiled extract. Visually there was hardly any seedling growth in this extract, most seedlings having only a minute coleoptile, and the radicle still enclosed in its sheath.

This marked inhibition of growth caused by the boiled extract contrasts with the relatively high germination obtained in it after illumination.

The anomalous behavior of the boiled extract could also be dependent on the short illumination which the units had received on the 4th day (cf. discussion in section "a" above). This was clari-

TABLE XIII. The effects of the inhibitory water-extract from intact dispersal units on germination and seedling growth at 20°C in uninterrupted darkness. Explanation in text

	Germination Medium								
	Water			Original extract			Boiled extract		
	Mean	Standard Deviation	Standard Error	Mean	Standard Deviation	Standard Error	Mean	Standard Deviation	Standard Error
Germination percentage									
on 4th day	*55.2*	5.2	2.3	*29.6*	3.9	1.8	*37.3*	2.9	1.4
on 7th day	*56.8*	7.0	3.1	*21.4*	4.6	2.0	*35.8*	14.2	6.3
Seedling weight (mg)									
on 4th day	*1.315*	0.075	0.033	*1.134*	0.046	0.023	*1.018*	0.041	0.018
on 7th day	*4.834*	0.389	0.168	*5.806*	1.116	0.499	*1.336*	0.181	0.081

fied in another experiment, similar to the previous one, except that the dishes counted on the last day (8th) were left in uninterrupted dark throughout the test period. Also, no dialyzed extract was used, and ungerminated units were not weighed this time.

The results (Table XIII) may be summarized as follows: (a) In uninterrupted darkness there was no additional germination after the 4th day, irrespective of germination medium. It is thus clear that all units which were capable of germinating in the dark had done so within that time. (b) Between the 4th and last day there was a large increase in seedling weight in water and the original extract (270 and 400%, respectively), but not in the boiled extract (30%). The external appearance of the seedlings grown in the boiled extract was similar to that in the previous experiment.

On the basis of the results from the two experiments it appears that the extract has the following properties:

(1) A short illumination stimulates dark-germination in water and in the original inhibitory extract, but does not remove the chemical inhibition. The latter inhibition is therefore unrelated to the light-sensitive mechanism in the dispersal unit.

(2) The inhibitory activity of the extract is greatly reduced by dialysis.

(3) The original extract does not inhibit seedling growth to any large extent. Seedlings growing in the extract achieve nearly the same fresh weight as those growing in water.

(4) A change occurs in the extract when it is boiled. It still inhibits dark germination to the same extent as when unboiled, but fails to do so with units which had been illuminated on the 4th day.

(5) After boiling, the extract becomes highly inhibitory to seedling growth, irrespective of continuous or interrupted darkness during the test.

These observations may be interpreted as follows: The extract contains an active germination inhibitor, and an inactive growth inhibitor. Both are apparently of small molecular weight. The properties of both are changed by boiling. The growth inhibitor is activated, and the germination inhibitor is no longer inhibitory to units which are stimulated by a short illumination.

The growth phenomena in germination

The growth inhibitor which is activated by boiling may be an artifact having no biological significance in nature. However, its activity may help to shed some light on the physiology of the germination process.

The successional phases in the germination process have been analyzed by Evenari (1957). The transition from the germination process to the growth process is usually recognizable by the protrusion of the growing radicle through the seed coat, which is in turn caused by cell division and cell growth. In the *Gramineae* the enveloping structures are breached by growth of the root sheath (coleorhiza), and later by the coleoptile. The seminal roots start their growth only after these preliminary steps. The coleorhiza is entirely composed of fully differentiated parenchymatous cells. As far as is known, these cells do not divide but merely grow in size during germination. It is this growth in cell size which results in the splitting of the pericarp during germination (Percival, 1921; Toole, E. H., 1940). Early growth of coleoptile and seminal roots consists of both cell division and cell growth. Those seedlings which had germinated in the boiled extract consisted of no more than a normal sized root sheath and a minute coleoptile. The fact that the root sheath had grown sufficiently to breach the pericarp is a clear indication that cell enlargement had taken place. By inference, then, cell division had been inhibited, resulting in a minute coleoptile and in arrested growth of other embryonic tissues depending on meristematic activity (e.g.

seminal roots). If that is indeed the case, the following interpretation is suggested for the physiological activities of the inhibitory extract. The growth processes of the preformed cells of the coleorhiza and coleoptile are the terminal phase of the germination process ("germinational growth"), differing basically from growth processes of cells recently formed by the meristematic activity in root apices and coleoptile, which are the initial phase of "seedling growth." The original extract contains an inhibitor A, which acts on the first of these growth processes, not on the second. Upon boiling, A is change to A* which is no longer inhibitory to light-stimulated units, and an inhibitor B* of the second of these growth processes is formed from an inactive B. These relationships are schematized in Fig. 10.

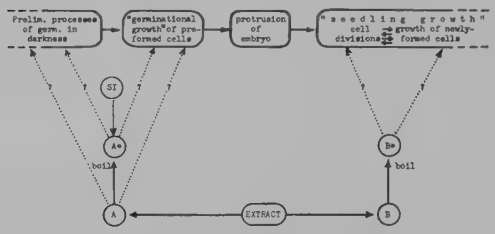


FIG. 10. Processes of germination which may be affected by the inhibitory extract (Schematic).

Germination is a succession of processes, many of which may be chemically inhibited or promoted (Evenari, 1957). The answer to the question whether germination inhibitors are at the same time growth inhibitors (Evenari, 1949) will therefore depend on such differentiation of growth processes as was found in *O. miliacea*. In the light of the above it would seem that substances A and A*, though inhibiting "germinational growth" of preformed cells, should not be classified as growth inhibitors since they do not affect seedling growth. Substance B*, on the other hand, despite being an artifact in a sense, seems to be a growth inhibitor without being a germination inhibitor.

As regards the relationships between A and B, only further investigation may tell whether they are one and the same, closely related, or completely independent substances.

SUMMARY

The germinability of dispersal units of *O. miliacea* was found to be relatively low in final percentage, and slow in rate. Optimal results were obtained 20°C/30°C daily temperature alternation.

Treatment with sulphuric acid (70% v/v) improved germinability, and units thus treated could be dry-stored without detrimental effects. Optimal duration of treatment varied between 20 and 40 minutes, and depended on the conditions under which the units had been stored prior to treatment.

Acid treatment did not affect water uptake by the dispersal units, but apparently removed an external layer of the caryopsis which contains a germination inhibitor.

Germinability of untreated units originating in arid habitats was markedly higher than of those originating in more humid habitats, and could be further improved by acid treatment.

Some of the above findings have been applied to reseeding practices in Israel.

Both temperature and light were effective in regulating germination. Constant conditions of light and dark imposed restrictions on germination, which were strongly temperature dependent. A single short illumination, applied between one and 28 days from sowing, removed the inhibition by darkness, making germination temperature-independent within the range tested (20°-30°C). Dispersal units which had been stimulated by a short illumination could be dried immediately after, without loss of stimulation.

The inhibition by constant conditions of light or darkness could be partially removed by a 20°/30°C temperature alternation. Even one such alternation sufficed to largely remove the inhibition by darkness at 20°C. The short illumination process is apparently independent of the alternating temperature process, though both are stimulatory to germination.

Thermal determination of germination in darkness by constant temperatures apparently comes into effect after the first 48 hours of imbibition.

The restrictions by constant light and constant dark to germination at constant temperatures were gradually modified with age.

The sensitivity to light was found in intact units as well as in acid treated ones, and is therefore not a result of the standard acid treatment to which they were subjected in order to increase germinability.

Some physical and physiological properties of the inhibitor in the dispersal units were investigated. The inhibitor is water-soluble, and could be gradually leached out of the caryopsis by simulated rainfall. The water-extract from intact dispersal units was equally inhibitory on germination in constant dark and after a short illumination, but did not affect seedling growth. After boiling, the extract maintained its inhibitory activity on dark germination, but was ineffective after a short illumination. The boiled extract was highly inhibitory to seedling growth. The osmotic value

of the extract and its pH are apparently not concerned with its inhibitory activity.

Some growth processes related to different phases of germination are discussed.

References

Biebel, J. P. 1942. Some effects of radiant energy in relation to etiolation. Plant Physiol. **17**: 377-397.

Black, M. and P. F. Wareing. 1955. Growth studies in woody species. VIII. Photoperiodic control of germination in *Betula pubescens* Ehrh. Phys. Plant. **8**: 300-316.

Bonner, J. and J. Liverman. 1953. Hormonal control of floral initiation. In: Loomis, W. E. (editor). Growth and differentiation in plants. Iowa State College, Ames.

Cohen, D. 1958. The mechanism of germination stimulation by alternating temperatures. Bull. Res. Council of Israel **6**: 111-117.

Crocker, W. and L. V. Barton. 1953. Physiology of seeds. Chronica Botanica Co., Waltham, Mass.

Evenari, M. 1949. Germination inhibitors. Bot. Rev. **15**: 153-194.

———. 1957. The physiological action and biological importance of germination inhibitors. In: The biological action of growth substances. Symposium Soc. Exp. Biol. **XI**: 21-43.

———. **and G. Neumann.** 1953. The germination of lettuce seed. III. The effect of light on germination. Bull. Res. Council of Israel **3**: 136-145.

Hamner, K. C. and J. Bonner. 1938. Photoperiodism in relation to hormones as factors in floral initiation and development. Bot. Gaz. **100**: 388-431.

Harder, R. and G. Gümmer. 1947. Über die untere kritische Tageslänge bei der Kurztagpflanze *Kalanchoë blossfeldiana*. Planta **35**: 88-99.

———., **E. Wallrabe and L. Quantz.** 1944. Über die Rolle der Temperatur bei der Zerstörung des Blühimpulses durch Zwischenbelichtung bei der Kurztagpflanze *Kalanchoë blossfeldiana*. Planta **34**: 41-48.

Harrington, G. T. 1923. Use of alternating temperatures in the germination of seeds. Jour. Agric. Res. **23**: 295-332.

Hayward, H. E. 1938. The structure of economic plants. McMillan. N. Y.

Isikawa, S. 1954. Light sensitivity against germination. I. "Photoperiodism" of seeds. Bot. Mag. Tokyo **67**: 51.

———. **and G. Shimogawara.** 1954. Effects of light on the germination of forest tree seeds. I. J. Japanese Forestry Soc. **36**: 318-323.

Kincaid, R. R. 1935. The effects of certain environmental factors on germination of Florida cigar wrapper tobacco seeds. Bull. Fla. agric. Exp. Sta. No. **277**.

Koller, D. 1955. The regulation of germination in seeds. Bull. Res. Council of Israel **5**: 85-108.

Lang, A. and G. Melchers. 1943. Die Photoperiodische Reaktion von *Hyoscyamus niger*. Planta **33**: 653-702.

Laude, H. M. 1951. Treatment to improve the emergence and stand of smilo grass. Jour. Range Management **4**: 88-92.

Lona, F. 1947. L'influenza delle condizioni ambientali, durante l'embriogenesi, sulla caratteristiche del seme e della pianta che ne deriva. Lavori de Botanica (G. Gola Jubilee vol., Padova, Italy): 313-352.

Long, E. M. 1939. Photoperiodic induction as influenced by environmental factors. Bot. Gaz. **101**: 168-188.

Mann, L. K. 1940. Effect of some environmental factors on floral initiation in *Xanthium*. Bot. Gaz. **102**: 339-356.

Morinaga, T. 1926. Effect of alternating temperatures upon the germination of seeds. Amer. Jour. Bot. **13**: 141-158.

Naylor, A. W. 1953. Reaction of plants to photoperiod. In: Loomis, W. E. (editor). Growth and differentiation in plants. Iowa State College, Ames. pp. 149-178.

Parker, M. W. and H. A. Borthwick. 1939. Effect of variation in temperature during photoperiodic induction upon initiation of flower primordia in Biloxi soybeam. Bot. Gaz. **101**: 145-167.

Percival, J. 1921. The wheat plant. A monograph. Duckworth, London.

Porter, R. H. 1949. Recent developments in seed technology. Bot. Rev. **15**: 221-344.

Seligman, N., N. H. Tadmor, Z. Naveh and J. Katzenelson. (In preparation.) A survey of natural pasture in Israel.

Soriano, A. 1953. Estudios sobre germinacion. I. Rev. Invest. agric. **7**: 315-340.

Stearns, F. and J. Olson. 1958. Interactions of photoperiod and temperature affecting seed germination in *Tsuga canadensis*. Amer. Jour. Bot. **45**: 53-58.

Stoddart, L. A. and K. J. Wilkinson. 1938. Induced germination in *Oryzopsis hymenoides* for range reseeding. J. Amer. Soc. Agron. **30**: 763-768.

Tadmor, N. H. and D. Hillel (Boguslav). 1956a. Survey of the possibilities for agricultural development in the southern Negev. Agric. Res. Sta. Rehovoth (Israel). Bull. **61**: 1-77.

———. 1956b. Observations on reseeding practices in water-spread areas in the Negev Highlands (southern Israel). Agric. Res. Sta. Rehovoth (Israel). Preliminary report No. **144**.

Taubman, H. 1953. Factors affecting the germination of *Oryzopsis miliacea*. M.Sc. Thesis, Hebrew University, Jerusalem, Israel. (In Hebrew.)

Toda, R. and H. Isikawa. 1951. Effect of diffuse light on the germination of *Paulownia* seeds. Jour. Japanese Forestry Soc. **34**: 250. (In Japanese.)

Toole, E. H. 1940. The transformation and course of development of germinating maize. Amer. Jour. Bot. **11**: 325-350.

———, **S. B. Hendricks, H. A, Borthwick and V. K. Toole.** 1956. Physiology of seed germination. Ann. Rev. Plant Physiol. **7**: 299-324.

———., **V. K. Toole, H. A. Borthwick and S. B. Hendricks.** 1955a. Photocontrol of *Lepidium* seed germination. Plant Physiol. **30**: 15-21.

———.,**V. K. Toole, H. A. Borthwick and S. B. Hendricks.** 1955b. Interaction of temperature and light in germination of seeds. Plant Physiol. **30**: 473-478.

Toole, V. K. 1939. Germination of the seed of poverty grass (*Danthonia spicata*). J. Amer. Soc. Agron. **31**: 954-965.

———. 1940. The germination of seed of *Oryzopsis hymenoides*. J. Amer. Soc. Agron. **32**: 33-41.

———. 1941. Factors affecting the germination of various dropseed grasses (*Sporobolus* spp. J. Agric. Res. **62**: 691-715.

Vaartaja, O. 1956. Photoperiodic response in germination of seed of certain forest trees. Canad. J. Bot. **34**: 377-388.

von Abrams, G. J. and M. E. Hand. 1956. Seed dormancy in *Rosa* as a function of climate. Amer. Jour. Bot. **43**: 7-12.

Walter H. 1931. Die Hydratur der Pflanze und ihre physiologischökologische Bedeutung. Jena.

Went, F. W. 1948. Thermoperiodism. In Murneek, A. E. and R. O. Whyte. Vernalization and photoperiodism. Chronica Botanica. Waltham. pp. 145-157.

———. 1952. The effects of rain and temperature on plant distribution in the desert. Desert Research. Proc. International Symposium (Special publ. No. 2. Res. Council of Israel) : 230-240.

———. 1953. The effects of temperature on plant growth. Ann. Rev. Plant Physiol. **4**: 347-362.

THE INFLUENCE OF GRAZING ON THE THIN-SOIL PRAIRIES OF WISCONSIN

RALPH L. DIX
Biology Department, Marquette University, Milwaukee, Wisconsin

The first European men to arrive on the prairies of Southern Wisconsin accepted the wild grasses, along with the abundance of game, as simply another part of a generously endowed landscape. Later immigrants, i.e., those arriving in the 1840's, were concerned chiefly with the production of wheat and only scant attention was paid to the forage value of the wild grasses. During these early years of agricultural settlement, the prairie grasses were utilized by only a few work animals and other livestock produced for home consumption. With the failure of the wheat crops in the early 1880's and the subsequent shift to the livestock economy, the wild grasses were at first abused to the point of destruction and then replaced wherever possible by cultivated pasture species. Some areas, such as sites too low and wet or too steep and dry, proved inhospitable to the cultivated species and were allowed to remain in native prairie. Within a few years, however, since little attempt was made to manage them for sustained yield, many prairies were severely overgrazed and invaded by weedy species, both introduced and native. Some prairies were reduced to relatively unproductive bluegrass (*Poa pratensis* and *P. compressa*) pastures and, through continued over-grazing, have remained in this condition to the present time. Other prairies have been less severely grazed and a few, due to accidents of ownership or topographic position, have escaped grazing altogether and retain their original vegetation.

Recent interest in grassland farming and pasture management has focused attention on the unproductive bluegrass pasture areas of the Lake States as sources of additional pasturage, and agronomists have turned to the native prairies as a reservoir of species which may be more productive than the bluegrasses in habitats unsuitable for intensive cultivation. As a means of investigating the use of native grasses and legumes in the pasture programs of the Wisconsin area, studies were begun on the agronomic characteristics of some promising native prairie plants. Some of this work has been reported by Robocker, *et al.* (1953), Archbald (1954), Robocker and Miller (1955) and Neiland and Curtis (1956).

The present study concerns the behavior patterns of plant species on the thin-soil prairies of Wisconsin under the influence of grazing. The approach to this problem has been the study of the plant community and its responses to grazing—i.e., an investigation of the numerical relationships between the component species of the thin-soil prairie community and the changes in these relationships which occur as grazing pressure becomes increasingly more severe. It is hoped that this rather theoretical study will help to bring about a better understanding of the behavior patterns of these species under grazing and will facilitate further study into their use in pasture and range programs. The present study makes no pretense at suggesting a management program for the thin-soil pastures of Wisconsin but rather it attempts to lay the theoretical groundwork for such a program.

The author wishes to express his sincere appreciation to the following persons who assisted in this study: to Dr. J. T. Curtis for advice in the development of the problem and for assistance in the preparation of the manuscript; and to Drs. John E. Butler and Orlin Anderson for invaluable assistance in the collection of field data. Finally, especial appreciation is expressed to my wife,

Agnes, for her assistance in many phases of the study.

The field work for this study was carried out during the summers of 1952, 1953, and 1954. The taxonomic nomenclature is according to Fernald (1950).

Description of the Area

The stands investigated in the present study (Fig. 1) lie mostly on the unglaciated plateau region of south central and southwestern Wisconsin. This dissected plateau is constructed of various dolomitic formations. In the glaciated areas of northern Dane, southern Columbia, eastern Green and Rock Counties, thin-soil prairies are found on outcrops which protrude through, and are, therefore, mostly independent of, the glacial till. Such outcrops are also exclusively of dolomite (Martin 1932).

Since one of the criteria for the selection of stands (see Methods) was that the modal soil depth be less than four inches, it follows that these prairies will have a soil profile composed of only the A and D horizons. The A horizon, although thin, has much the same characteristics as its counterpart on the deeper soil prairies. The thin-soil prairies are usually found on outcrops and stand above the general landscape; they occur

Fig. 1. Map of Wisconsin showing the location of the stands studied. Each dot represents the location of an ungrazed-grazed pair of stands.

on slopes (6 to 25 degrees) and are excessively drained. Upon weathering, these D horizons yield a soil very rich in mineral nutrients with pH values in excess of 7.5. In western Wisconsin, eastern Iowa, and southeastern Minnesota, such soils are classed as the Sogn-Dolomitic Rock Outcrop Complex of the Fayette-Dubuque Series or sometimes simply as "stony lands" (Hole *et al.* 1952).

The climate of this area and its relationship to the vegetation have been extensively treated by Transeau (1935) and Borchert (1950). In general, it may be said that the region is characterized by a continental type of climate; the winters are cold (January average 12-15° F.) and the summers are quite warm (July average 70-72° F.). The total precipitation, although subject to serious fluctuations, averages about 30-32 in. per year, with July as the month of heaviest rainfall. The growing season averages about 160 days in the north and about 10 days more in the vicinity of the southernmost stand.

The prairies of Wisconsin lie along the northeastern edge of the prairie peninsula as described by Transeau (1935). These prairies may be grouped into several general topographic types (wet, mesic, and dry), which grade imperceptibly from one type to the other as moisture conditions change with topographic position. The chief dominant of the Wisconsin prairies is *Andropogon gerardi,* which occurs as a dominant in all prairie types of the state. Other dominants, in order of their importance from wet to dry topographic sites are *Calamagrostis canadensis, Spartina pectinata, Sorghastrum nutans, Stipa spartea, Sporobolus heterolepis, Andropogon scoparius,* and *Bouteloua curtipendula.* At the wet end of this gradient, the prairies gently grade into the sedge meadows and marshes while at the other extreme, the thin-soil prairies occupy the driest sites of the state.

In studies on the phytosociology of the dry prairies, Anderson (1954) obtained presence data from 64 and frequency data from 41 stands located in southcentral and southwestern Wisconsin. He concluded that a great deal of uniformity exists among the dry prairies with regard to species composition and soil factors. Curtis (1955), working with the entire moisure gradient on which prairies occur in Wisconsin, arranged 157 stands, which were located in 37 counties, along a moisture gradient by calculating the relative occurrence of certain indicator species in each stand. These indicator species were chosen on the basis of high percentages of occurrence in a topographic type. The ten indicator species of the "dry prairies," roughly the same stand types as the "dry lime prairies" of Anderson (1954) and the thin-soil prairies sampled in the present study, were found to be: *Andropogon scoparius, Anemone patens, Arenaria stricta, Artemisia caudata, Aster*

ptarmicoides, Aster sericeus, Bouteloua curtipendula, Panicum perlongum, Petalostemum purpureum, and *Solidago nemoralis.*

Methods

Choice of stands

The design of the present study was to utilize pairs of stands in which the partners were identical with the exception that one member of each pair had been grazed while its partner remained ungrazed. In this way the grazed stand served as the "treatment" and its ungrazed partner as the "control." It was not difficult to locate grazed prairies for this study but ungrazed prairie sites were difficult to find. The area under study is in a region of intensive agriculture and it is only through some accident of ownership or land use that undisturbed remnants of the native prairie have remained. In the course of three summers' field work, however, twenty-four pairs of stands were located which met the criteria for stand selection given below.

The original plan was to study the effects of grazing on all prairie types found in Wisconsin. It was soon discovered, however, that although there were pairs of stands available for the wet and dry prairies, none could be located for mesic sites. This is because the rich, deep soil of the mesic prairies is too valuable to remain in unimproved pasture and is always plowed and planted to more productive crops. The wet and dry prairies, however, because they can be put to no more profitable use, are fenced and used as unimproved pasture. For these reasons, the attempt to study the mesic prairies was given up, and, since this divided the prairie into two distinct and vegetatively distant parts, the wet prairies were also abandoned and attention focused on the dry, thin-soil group.

The ungrazed prairie stands to be used in the study were selected on the basis of the following criteria: (1) The stand must contain at least thirty plant species listed on a previously prepared catalogue of the vascular plants occurring on the undisturbed prairies of Wisconsin. (2) The stand must have a median soil depth of four inches or less. (3) The stand must show no signs of disturbance, such as grazing, plowing, or mowing.

Since the ungrazed prairies were by far the more difficult to locate, they were the first consideration in stand selection. When such a prairie was found, a partner for it was sought which met the following criteria: (1) The stand must be on the same type of site as its prairie partner; i.e., must have approximately the same slope, exposure, and soil depth. (2) The stand must show no evidences of plowing, fertilization, or other renovation processes. (3) The stand must be adjacent to, or within one-quarter mile of, its partner.

Regardless of the total size of the prairie or pasture stands, only comparable parts of the partner stands were used.

Field methods

The frequency index, when determined by the use of quadrats, is one of the simplest and most rapid tools available to the phytosociologist. Moreover, the many problems connected with estimating cover or counting individuals, which are almost insurmountable in grassland communities, are avoided. Since its introduction by Raunkiaer (1909), the characteristics of this index have attracted the attention of many investigators and Goodall (1952) has reviewed this extensive literature. The general conclusion of these researches is that frequency data, when obtained with an adequate number of samples, and when the samples are objectively located throughout the stand, are reproducible and, therefore, represent some actual characteristic of the vegetation. Curtis and McIntosh (1950) have suggested that the most practicable size for the study quadrat, when frequency determinations are to be made, is one which will give frequencies of approximately 86% for the most common species.

Field trials on the thin-soil prairies of Wisconsin have indicated that the one-quarter square meter quadrat will yield frequencies reasonably close to the figure suggested by Curtis and McIntosh.

In the early stages of the study, seven pairs of stands were sampled by the use of 80 one-quarter meter quadrats per stand. Upon examination of these data, it was found that approximately the same frequencies were obtained by the use of forty as with sixty or eighty quadrats; consequently, the number of samples per stand was reduced to forty. Thus, each of the forty-eight stands was sampled with at least forty quadrats of a size one-quarter square meter.

The vegetation was sampled by placing the quadrats at the ends of predetermined pace distances (usually 15 or 20 paces) along several lines laid out in such a way that the entire sample area was represented. Plants which could not be identified in the field, usually because of immaturity, were tagged and brought back to the University of Wisconsin Herbarium for comparison with labeled specimens.

Soil samples were collected by digging small soil pits in three widely separated areas of the stand. A soil sample was taken from the first inch

at each station and the three samples pooled. The pooled samples were prepared for analysis by forcing them through a 2 mm. screen. A part of each sample was used to determine water retaining capacity by employing the standard Hilgard cups while the remaining part was sent to the Wisconsin State Soil Testing Laboratory for analysis. These samples were analyzed for available calcium, magnesium, phosphorus, potassium, NO_3 NH_4, and the pH values were determined.

Treatment of data

The well known mathematical relationship between frequency and density was utilized to convert the frequency data to density. The table presented by Fracker and Brishchle (1944) was used in this conversion. This relationship, of course, holds exactly only for those species with random distributions. However, it has been shown (Steiger, 1930; Clapham, 1936; and Anderson, 1954) that not all prairie species are dis-

TABLE I. The original data, in plants per ¼ sq. M. (minimum densities) for the twenty-two most important species of the study. The species list is arranged with the highest positive grazing susceptibility number at the top and the lowest negative grazing susceptibility number at the bottom of the column. The stands are arranged according to their stand index numbers. *Viola* spp. = *V. pedata* + *V. pedatifida*

Stand index No.	+604	+551	+537	+520	+509	+473	+453	+441	+381	+375	+355	+322	+316	+296	+280	+266
Stand No.	7P	21P	9P	22P	3P	5P	1P	23P	4P	14P	13P	24P	20P	25P	15P	2P
Sporobolus heterolepis	.31	.16	.23	.14	.18	.46	.25	.16	.10	.63	.30	.12	.18	.07	.35	.12
Liatris cylindracea	.54	.02	.02			1.20	.04	.60	.29		.04	.91	.12		.22	.38
Sorghastrum nutans	.17	.16	.54	.40	.60	.05	.77	.10		.10	.15	.35	.02		.35	.07
Euphorbia corollata	.51	.07	1.23	.18	.38	.12	.15	.22	.69	.51	.16	.02	1.05	.02	.69	.10
Amorpha canescens	.84	.84	.17	1.56	.18	.02	.01	.29	1.05	.16	.35	.18	.16	.16	.05	.31
Viola spp.	.09	.05	.17			.73	.82	.46	.35	.02	.06	.12	.02	.07	.05	.46
Andropogon gerardi	.31	1.39	.94	1.56	1.71	2.04	.30	.31	1.47	.05	.65	.60	.73	.80	.51	.91
Petal stemum purpureum	.15	.16	.05	.51		.05	.30	.10	.05	.16	.33	.07		1.47	.22	.10
Aster sericeus	.35	.43	.54	.40	.02	.54	.82	.43	.18	.12	.62	.51	.46	.02	.10	..
Panicum prel ngum	.25	.35	.01	.22	.10	.07	.13	.43	.12		.22	.29	.05	.10	.29	.12
Andropogon sc parius	.21	1.05	2.04	.99	1.47	1.61	3.50	2.99	1.39	1.11	.60	1.89	.73	2.30	.60	.43
Aster azureus	.15	.29	.43	.51	.54	.80	.71	.02	.54	.05	.15	.16	.05	.22	.16	1.27
Solidag nem ralis	.02	.05	.02	.03	.02	.12	.58	.31	.12	.02	.05	1.11	.07	.38	.10	.43
Bouteloua curtipendula	.12	.51	.09	.51	.38	.63	.56	.84	.96	1.05	1.39	.91	.38	.60	1.61	.73
Asclepias verticillata			.01		.16					.10	.01		.46		.16	.05
Poa pratensis	.15		.58			.35	.04		.38	.16	.27	.05	.60			.91
Poa compressa	.87		.07		.02	.02	.01		.51	.96	.65	.02	.25		.51	.16
Ambrosia artemisiifolia	.01						.01			.02						
Agrostis alba																.10
Artemisia frigida		.02										.07				
Taraxacum officinale	.06															
Trifolium repens																

Stand index No.	+233	+230	+209	+173	+169	+163	+146	+135	+65	+31	−9	−42	−120	−136	−164	−183
Stand No.	12P	16P	23G	18P	8P	22G	19P	17P	4G	16G	10P	11P	15G	13G	9G	25G
Sporobolus heterolepis	.05	.05		.43	.02	.07	.05	.16		.05		.03				.02
Liatris cylindracea				.29	.06		.05	.91	.05		.23	.11				
Sorghastrum nutans			.10	.29	.02										.25	
Euphorbia corollata	.51	.10	.16	.69	.07	.26	.16	.05		.05	.11	.27	.05		.05	
Amorpha canescens	.69		.51	.16	.02	.18	.29	.05	.05	.22	.21	.16				.07
Viola spp.	.22	.10	.60	.05	.10			.05	.35	.05		.03			.02	.07
Andropogon gerardi	1.20	.69		.29	.18	1.96	.43	.69	.35	.51	.05	.17	.05		.18	.25
Petalostemum purpureum	.05	.35	.60		.01	.14	.05	.51		.10	.08	.06		.01	.06	
Aster sericeus			.60	.16	.41	.03	.29	.60	.05	.15	.60	1.39		.41		.07
Panicum prel ngum	.35		.22	.10	.07			.22	.38	.05	.21	.33	.10		.05	.60
Andropogon scoparius	.91	.10	2.99	1.05	1.27	.56	2.99	1.39	2.30	.43	.26	.23	1.61	.58	.89	1.05
Aster azureus	.05		.22	.43	.05			.05	1.47	.10	.08		.60	.43	.52	.02
Solidago nemoralis	.35		1.20	.35		.03	.22	.43	1.39	.43	.20	.77	.51	.22	.04	.43
Bouteloua curtipendula	.80	.91	1.61	.51	.15	.69	1.20	.91	1.71	.51	1.39	.52	2.99	1.05	.58	.29
Asclepias verticillata	.22	.10	.22	1.05	.02	.07	.29	1.05	.02	.43	1.08	1.77	.35	.09	.09	
Poa pratensis	.69	1.61	.05	.22	1.23	.56	.10	.22	.07	1.20	.51	.52		.43	.51	.43
Poa compressa	.22	.05		1.05	.21		.43	.35	.05	1.39	.56	.49	1.89	1.17	.77	
Ambrosia artemisiifolia	.05	.10			.01	.03	.16	.10			.17	.27	.22	.10	.18	
Agrostis alba															.09	
Artemisia frigida																1.27
Taraxacum officinale									.02	.10					.09	
Trifolium repens					.01						.04			.03	.43	

TABLE I. (Continued)

Stand index No.	-190	243	-245	-272	-289	-356	-371	-421	-441	-454	-459	-461	-521	-756	-771	-779
Stand No.	19G	1G	5G	20G	14G	11G	18G	17G	21G	3G	24G	12G	10G	8G	7G	2G
Sporobolus heterolepis			.05		.05									.01		
Liatris cylindracea	.05	.03	.02				.22	.05						.01		
Sorghastrum nutans									.02							
Euphorbia corollata	.29	.03				.01	.29					.10	.03			
Amorpha canescens					.29				.03				.06		.02	
Viola spp.		.40	.02							.02	.05		.03	.05		
Andropogon gerardi	.35		.12		.10	.03			.02	.07	.02		.10	.04	.10	
Petalostemum purpureum	.22	.05		.16	.16	.17	.05		.02		.02		.03			
Aster sericeus	.10	.18	.07	.22		.33	.35	.05	.31	.12			.08			
Panicum prelongum	.05	.01	.29	.10		.03	.05	.05	.02		.02		.04		.01	
Andropogon scoparius	.60	.21	1.71	.35	.51	.23	.16	.05		.07	.25		.11			
Aster azureus	.10	.25	.02	.05	.05	.03	.22	.22	.10	.22			.10		.01	.02
Solidago nemoralis	.51	.25	.10	.22	.10	.94	.60	.60	.51	.02	.22	.05	.15			
Baudelonia curtipendula	1.05	1.02	2.99	.91	1.89	1.05	1.89	.43	1.11	3.51	1.11	.22	.99	.21	.16	.35
Asclepias verticillata	.43	.82	.10	.43	.60	1.31	6.91	2.30	.02	.10	.02	.60	1.17			.02
Poa pratensis	1.61	.26	.60	1.89	.51	1.23	.10	2.30	.18	.18	.29	1.20	.33	.49	2.40	.60
Poa compressa	.35	.04	.80	.35	1.61	.33	2.30	.43	.69	3.51	.35	.91	1.20	.37	.84	.69
Ambrosia artemisiifolia	.13	.08		.22	.22	.60	.10		.29	.91	.10	.10	.71	.04	1.20	.38
Agrostis alba	.05		.02											2.52	.35	1.20
Artemisia frigida									1.11		2.04					
Taraxacum officinale			.05		.10	.03			.05	.05			.23	3.22	2.04	1.89
Trifolium repens					.35	.27		.05	.35				.77	2.04	2.52	.02

tributed at random but that many species are aggregated. Curtis and McIntosh (1950), working on artificial populations, have indicated that frequency values are too low for any given density if the species has an aggregated distribution. Thus, density values, as calculated from frequency data, are in reality *minimum density values;* they say, in effect, that a species has at least the indicated density but, if it is an aggregated species, its actual density may be greater.

All further calculations are in terms of minimum densities; since the quadrat size used was one-quarter square meter (each side 0.5 meter), the density figures given are the number of plants per one-quarter square meter.

RESULTS

As a first step in the analysis of the data (Table 1), attention was given to the leading species of the individual ungrazed prairie stands. Eight different species were found to have the highest densities in at least one of the twenty-four stands studied. An examination of the first two leading species in each stand showed 19 different combinations, while, when the first three leaders were considered, every stand had a different arrangement. Because of the highly variable nature of these ungrazed prairies, it appeared that no idealized species composition could be objectively assigned as the "climax community" (Dyksterhuis, 1949). Further, since the grazed stands showed similar variations, there seemed little justification for assuming that the condition of a grazed stand could be determined by contrasting it with such an idealized climax composition. A more promising approach seemed to lie in ascertaining the behavior of individual species under the impact of various degrees of grazing pressure; the condition of a grazed stand could then be judged in the light of the behavior patterns of its component species. A method was sought, therefore, which would objectively indicate the behavior of each species under grazing pressure.

Since the stand pairs were selected in the field so that the only discernible difference between the members was grazing, and since the grazed members were in various stages of degeneration, it was felt that the behavior of species under grazing pressure could best be determined by mathematical comparisons between the stand pairs. This comparison was carried out by summing the densities for each species in the grazed and ungrazed stands separately. The sum of densities for the pasture stands was then subtracted from the sum of densities for the ungrazed prairies regardless of which number was the larger. When the sum of densities was larger in the ungrazed stands, then this was a positive number; when the reverse was true, it was a negative number. When this algebraic difference was a positive number, it was divided by the sum of densities for the ungrazed stands or, when a negative number, by the sum of densities for the grazed stands.

To facilitate their use in further calculations these index numbers were multiplied by 10, to avoid the use of decimals, and rounded off to one digit. Since numbers calculated in this way indicate the phytosociological behavior of a species

under grazing pressure, they have been given the name grazing susceptibility numbers. The procedure for finding these numbers may be summarized by the formula:

$$\text{Grazing Susceptibility Number for species A} = \frac{\text{Sum Densities Ungrazed} - \text{Sum Densities Grazed}}{\text{Sum Densities Ungrazed}} \times 10$$

$$\begin{bmatrix}\text{when numerator is}\\ \text{positive}\end{bmatrix} \quad or \quad \begin{bmatrix}\text{when numerator is}\\ \text{negative}\end{bmatrix}$$

For example, the grazing susceptibility number for *Andropogon scoparius* was calculated as follows: the sum of densities in the ungrazed and grazed stands were found to be 31.95 and 19.85, respectively. Therefore:

$$\text{G.S.N.} = \frac{31.95 - 19.85}{31.95} \times 10 = .37 \times 10 = 3.7$$

The figure 3.7 was rounded off to 4 to expedite further calculations. Thus, the grazing susceptibility number for *Andropogon scoparius* was calculated to be plus 4.

Index numbers calculated in this way have limits of plus 10 in cases where a species is found only in ungrazed stands (algebraic difference = sum of densities ungrazed), to minus 10 where a species is found only in the grazed stands (algebraic difference = sum of densities grazed). These index numbers approach O as the algebraic differences approach O; the index number is O when a species has the same sum of densities in both types of stands. These numbers, therefore, indicate the relative change in the density of a species brought about by grazing pressure.

Grazing susceptibility numbers were calculated for all species which had a frequency of two percent or more in either the grazed or ungrazed set of stands (Table II).

The grazing susceptibility numbers derived in the present study may be interpreted as an estimation of the ability of the species to withstand the environmental and biotic conditions brought about by livestock grazing. A relatively high plus number indicates that a species is hampered or is at some disadvantage under grazed conditions while, conversely, a relatively large minus number indicates that a species is benefited by a grazed environment. Negative grazing susceptibility numbers do not imply, however, that a species is benefited by the removal of a part of its top growth by livestock; they do imply that the changes which take place in the environment and biotic composition under grazing permit the species to increase. Thus, the grazing susceptibility numbers are applicable only within the framework of their derivation and may not hold in other environments or with other associated species. Dyksterhuis (1946), for example, found *Bouteloua curtipendula* to be a decreaser in southwestern Texas while in the present study it was found to be an important increaser.

The grazing susceptibility numbers were then used to weight the relative density values as a means of ordering the stands. This was done by multiplying the relative density value of each species in each stand by its grazing susceptibility number. These figures were then summed to give a single number, the stand index number, which represents the relative position of a stand along the grazing gradient. A stand composed mostly of species with negative grazing susceptibility numbers will have a negative stand index number or, if composed mostly of species with positive grazing susceptibility numbers, a positive stand index number. Such stand index numbers have theoretical limits of plus 1,000 and minus 1,000.

Stand index numbers were then calculated for the forty-eight stands of the study and the stands arranged in a linear fashion according to their stand index numbers (Fig. 2). In this figure the ungrazed stands are indicated by marks above the base line while grazed stands are shown as marks below the base line. It is apparent that all but two of the ungrazed stands have plus and all but four of the grazed stands have minus stand index numbers. Upon examination, it was found that in every case the grazed partner of a stand pair was to the right of its ungrazed partner. The grazed stand at plus 209, for example, is the partner of the ungrazed stand at plus 441. In the case of ungrazed stands with minus stand index numbers, it was found that these stands were composed mostly of native prairie species which increase under grazing, such as *Bouteloua curtipendula*, and a few such stands would be expected to occur even without grazing.

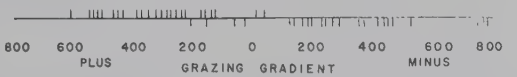


FIG. 2. Arrangement of all stands according to their stand index numbers. Marks above the base line represent ungrazed stands while marks below the base line indicate grazed stands.

As a means of finding the behavior of individual species along this phytosociological grazing gradient, the densities of each species were plotted against the gradient as has been done for *Bouteloua curtipendula* in Figure 3. The scatter diagram has been presented to show the typical varia-

TABLE II. Grazing susceptibility numbers for the seventy-eight most common species[1] of the study

PLUS		MINUS	
Aster laevis	10	*Potentilla argentea*	10
Pedicularis canadensis	10	*Erigeron canadensis*	10
Hypoxis hirsuta	10	*Trifolium repens*	10
Phlox pilosa	10	*Taraxacum officinale*	10
Polygala senega	10	*Oxalis stricta*	10
Monarda fistulosa	9	*Agropyron repens*	10
Dodecatheon meadia	9	*Artemisia frigida*	10
Sporobolus heterolepis	9	*Agrostis alba*	10
Liatris cylindracea	9	*Euphorbia maculata*	9
Lithospermum canescens	9	*Plantago major*	9
Physalis heterophylla	9	*Achillea millefolium*	9
Sorghastrum nutans	9	*Verbena stricta*	8
Silphium laciniatum	9	*Ambrosia artemisiifolia*	8
Lobelia spicata	9	*Hedeoma hispida*	8
Zizia aptera	9	*Trifolium dubium*	7
Panicum leibergii	9	*Melilotus* spp.	7
Helianthus occidentalis	9	*Poa compressa*	6
Helianthus laetiflorus	8	*Antennaria* spp.	6
Euphorbia corollata	8	*Poa pratensis*	6
Coreopsis palmata	8	*Asclepias verticillata*	6
Comandra umbellata	8	*Erigeron strigosus*	5
Anemone cylindrica	8	*Bouteloua curtipendula*	4
Amorpha canescens	8	*Lithospermum incisum*	3
Stipa spartea	8	*Castilleja sessiliflora*	3
Viola spp.	7	*Solidago nemoralis*	2
Andropogon gerardi	7	*Aster pilosus*	2
Potentilla arguta	7	*Panicum oligosanthes*	1
Petalostemum purpureum	6	*Bouteloua hirsuta*	1
Sisyrinchium campestre	6	*Artemisia caudata*	1
Physalis virginiana	6	*Solidago speciosa*	1
Aster ptarmicoides	6		
Aster sericeus	6		
Liatris aspera	5		
Ratibida pinnata	5		
Aster oblongifolius	5		
Panicum perlongum	4		
Muhlenbergia cuspidata	4		
Carex spp.	4		
Andropogon scoparius	4		
Rosa sp.	3		
Aster azureus	3		
Aster ericoides	2		
Anemone patens	2		
Linum sulcatum	2		
Scutellaria parvula	1		
Kuhnia eupatorioides	1		
Arenaria stricta	1		
Solidago rigida	1		

[1] The species within some genera were not distinguishable at all seasons of the year: *Viola* spp. = *V. pedata* and *V. pedatifida* while *Melilotus* spp. = *M. alba* and *M. officinalis*. *Carex* spp., *Rosa* sp. and *Antennaria* spp. represent plants whose taxonomy in this areas has not been clearly established.

tion of a species from stand to stand while the smooth curve demonstrates the general behavior of the species along the grazing gradient. This smooth curve was derived by grouping the data into 100 unit intervals and then smoothing by the formula: $a + 2b + c/4$. These smoothed points were then plotted on a graph and further smoothed by inspection. It is evident from the scatter diagram presented in Figure 3 that, due to various

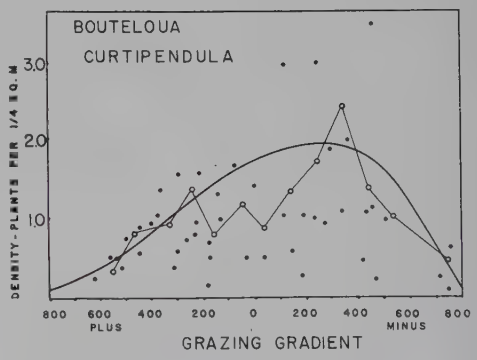


FIG. 3. Method of smoothing data for *Bouteloua curtipendula*. The solid circles denote density values in the individual stands. The open circles represent the same values averaged for 100 unit intervals along the grazing gradient. The open circles were smoothed by the formula discussed in the text and the smooth line drawn by inspection through these points. The obtained smooth curve is thought to represent the behavior of *Bouteloua curtipendula* along the grazing ecocline.

chance situations, even in a stand where environmental conditions are apparently optimum, a species may be absent or in low numbers, while, in another very similar stand, the same species may be a dominant. However, a species tends to be less important in stands far removed from its optimum. Similar Gaussian curves were obtained by Curtis and McIntosh (1951) and Brown and Curtis (1952) in studies on Wisconsin forests. Graphs for twelve of the leading species are presented in Fig. 4, and density data for the leading species are given in Table I.

If the phytosociological gradient presented above is a grazing gradient, the order of the ungrazed stands necessitates further explanation. Since these stands were not grazed, the term "grazing gradient" perhaps seems a misnomer. In an effort to examine the nature of this gradient, a comparison was made between the grazing susceptibility numbers (Table II) and the index numbers derived by Curtis (1955). Curtis, working with ungrazed stands of all prairie types in Wisconsin, assigned index numbers to fifty indicator species on the basis of high presence values in a topographic prairie type. A species which had its highest presence in the wet prairies was assigned the index number 1, while a species with its highest presence values in the dry, thin-soil prairies were given the number 5. Intermediate species were given intermediate index numbers.

The relative density of each species in each ungrazed stand was multiplied by Curtis' index number to give a weighted figure. These figures were then summed and divided by the number of

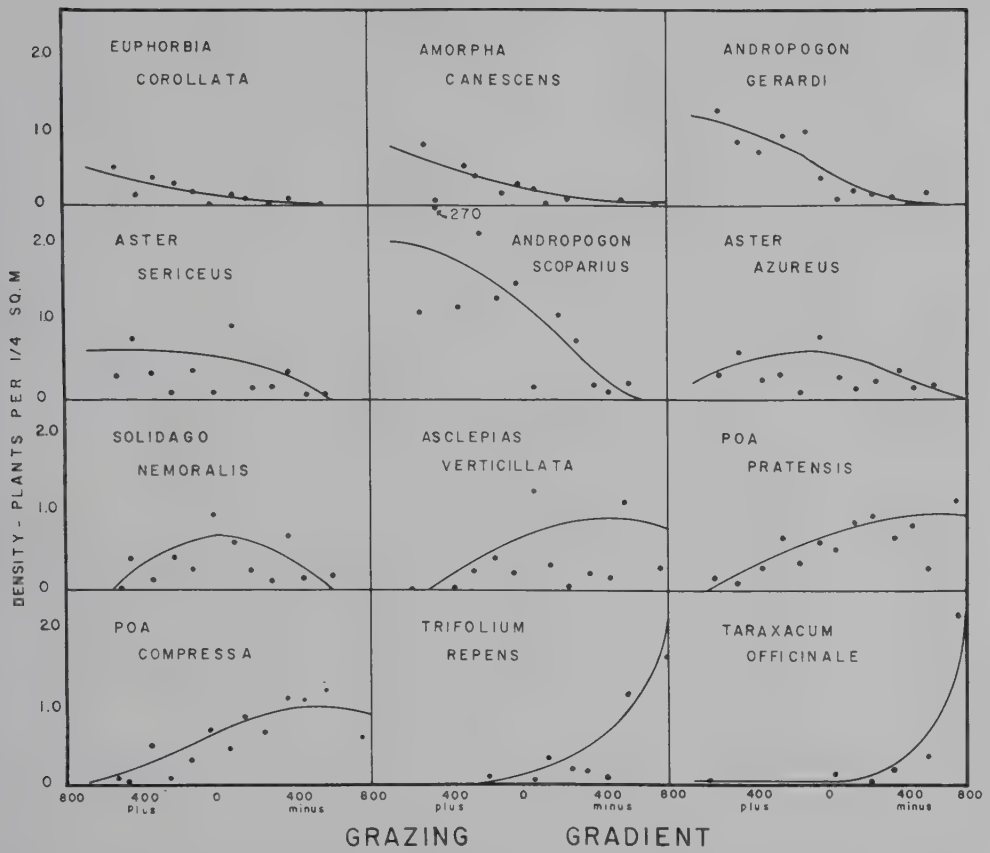


FIG. 4. Behavior of selected species when plotted against the grazing gradient. The dots represent density values averaged by 100 unit intervals. The smooth curves were obtained by the methods illustrated in Figure 3.

indicator species that had occurred in the quadrats of that stand. In this way one figure was again obtained to represent each ungrazed stand. The stand index numbers, as calculated by use of the grazing susceptibility numbers, were then plotted against the stand index numbers as calculated with the indicator species of Curtis. The grazed stands were not used in this comparison because they had few, and in some cases none, of the indicator species. The relationship between these two sets of index numbers indicated, that, in Figure 2, the ungrazed prairies to the left were more mesic than those to the right. The terms "mesic" and "dry" are here relative since all of the stands in the present study range only from "mesic-dry" to "dry" in the nomenclature of Curtis (1955).

It is well established that the predominantly upright growth habit of the Tall-Grass Prairie species renders them highly susceptible to grazing by livestock. Conversely, the rhizomatous or often prostrate growth form of the more xeric species make them comparatively more resistant to grazing. It is not surprising, therefore, to find that the more mesic stands of the present study are composed chiefly of species which decrease under grazing pressure while the more xeric stands are composed of many species which increase. Such erect species as *Sorghastrum nutans* and *Sporobolus heterolepis,* for example, have their highest densities in the mesic-dry ungrazed stands while low growing forms, such as *Bouteloua curtipendula,* have higher densities in the dry ungrazed stands and often obtain their highest densities in slightly to moderately grazed stands.

In summary, it may be said that, since the grazing susceptibility numbers (Table II) were derived in such a way that only the relative changes in density brought about by livestock grazing were considered, the grazing susceptibility numbers appear to have no direct relationship to the moisture requirements of the species. However,

the relationship between the moisture requirements of a species and its growth form, and therefore, its ability to withstand grazing, is well established in the literature and is evident in the present study. Thus, when the grazing susceptibility numbers were used to order the stands along a grazing gradient, they secondarily ordered them along a moisture gradient. It seems justifiable, therefore, to consider the phytosociological gradient established by use of the grazing susceptibility numbers as primarily a grazing gradient.

Comparisons were also made between the ungrazed prairie stands and their grazed partners. From an inspection of Figure 2, an obvious approach would be to measure the distance along the grazing gradient between the members of a stand pair. A low distance number would indicate that grazing had moved the grazed stand only slightly to the right while a high distance number would indicate that considerable phytosociological change had taken place in the grazed stand. A graph was then constructed (Fig. 5)

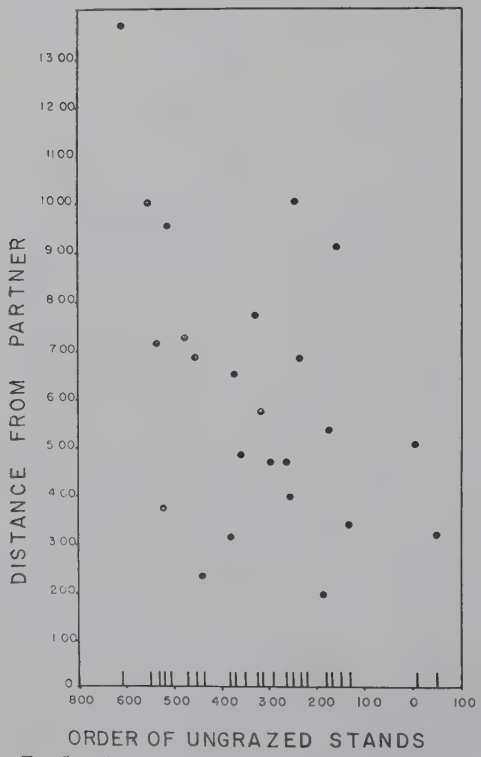


FIG. 5. The phytosociological distance between the ungrazed stands and their grazed partners. Marks above the base line represent the ungrazed stands as in Figure 2. Note the decrease in distances towards the dry (right) end of the gradient.

in such a way that the abscissa represented the stand order of only the ungrazed stands (Fig. 2), which had previously been shown to be a moisture gradient, and the ordinate the distance of the grazed stands from their partners. For example, the distance between the partners of Stand 21 is 992 (Table I), and between the partners of Stand 16, 199.

Figure 5 does not show a random distribution of grazed stands as would be expected if each had the same chance to be heavily or lightly grazed. Conversely, there is a noticeable decrease in the distance between partners toward the drier end of the gradient. This is in agreement with the phenomenon described above where the more xeric species are less susceptible to grazing injury than are the more mesic species.

Soil analysis data were available for six soil nutrients (Ca, P,K. Mg, NO_3, and NH_4), pH and water retaining capacity of the A_1 soil horizon. When these data were plotted against the phytosociological grazing gradient all soil factors proved to be highly variable and no trends were evident. The mean values for these soil factors in the grazed and ungrazed stands are presented in Table III. When standard error tests were ap-

TABLE III. Average soil nutrients and water retaining capacities in the grazed and ungrazed stands. The differences between these values proved to be not significant at the five percent level when standard error tests were applied. Soil nutrient data are given in pounds per acre while the water retaining capacities are in percent

	Ungrazed	*Grazed*
Calcium	9,700	10,150
Magnesium	1,110	1,295
Nitrate	5.5	6.1
Ammonia	18.7	15.2
Phosphorus	75	88
Potassium	181	176
Water Retaining Capacity	90%	74%

plied the differences between these values proved to be not significant at the five percent level. The absence of any correlation between the soil nutrients and the grazing gradient would appear to indicate that these soil nutrients are present in all stands in amounts sufficient to permit good growth conditions for all important species. The lack of any correlation between the water retaining capacity of the A_1 soil horizon and the grazing gradient is possibly due to the narrow limits imposed by the soil criteria used in the selection of the stand.

DISCUSSION

The deterioration of the native thin-soil prairies to bluegrass pastures under grazing has been shown in the present study to follow a continuous

downward curve from climax vegetation. In ungrazed to slightly grazed prairies *Andropogon gerardi, A. scoparius, Sorghastrum nutans* and *Sporobolus heterolepis* dominate. As the vigor of these species is reduced by grazing, less susceptible species, *Bouteloua curtipendula* and *Solidago nemoralis* among others, increase rapidly and the former is usually dominant in moderately grazed stands. If grazing is further increased, these species yield to the bluegrasses. The bluegrasses appear able to withstand heavy grazing pressure and, as indicated by their behavior curves in Figure 4, reach their best development in the most severely grazed pastures sampled in this study. However, observations on other areas (feedlots, around gates, etc.) indicate limits to their persistence under grazing. In such cases the bluegrass sod breaks up, soil erosion begins, and the area supports only scattered individuals of weedy forbs and grasses.

The above sequence is most accurately described in terms of the phytosociological behavior, under grazing, of the component species. It has become a widely used practice in grazing studies to assign each species to one of three behavior groups based on their responses to grazing: decreasers, increasers and invaders (Smith, 1940; Daubenmire, 1940; Weaver and Hansen, 1941; Voight and Weaver, 1951; Dyksterhuis, 1948, 1949; and Lauchbaugh, 1955). It was found in the present study, however, that not all species fit clearly into one of these categories but that each had its own characteristic behavior which was sometimes similar to, but never exactly like, that of any other species. The formula for the derivation of the grazing susceptibility numbers produced at least one species for each susceptibility number class (Table II) and there seemed little tendency for the species to form discrete behavior groups. Thus, while the terms decreasers, increasers and invaders are convenient categories they appear limited in ecological meaning. *Aster laevis* and *Andropogon scoparius,* for example, would both be classified as decreasers on the thin-soil Wisconsin prairies although the former is far more sensitive to grazing. It is suggested, therefore, that the use of these terms be restricted to their adjectival meaning; they could then be used to describe the general behavior patterns of species without the misleading implication of pigeon-hole categories.

Weighted index numbers have been used to describe the ecological behavior of plant species by a number of workers (Ellenberg, 1948, 1950; Curtis and McIntosh, 1951; Whittaker, 1952; and Curtis, 1955). The internal proof that the assigned index numbers represent the behavior of the species with relation to each other is in the appearance of relatively smooth curves when the importance values (e.g., densities, frequencies, cover, etc.) for the individual species are plotted against the phytosociological arrangement of stands formed by the use of the index numbers. When these importance values are smoothed by accepted statistical methods the general behavior patterns of the species along a particular gradient become evident and the variations in population numbers, due to other variables of the environment, to species diversity, and to chance, tend to be averaged out and their behavior against a particular gradient demonstrated. In the present study, each of the species behavior curves (Fig. 4) are seen to be different although in every case the curve is found to be bell-shaped or some part of such a curve. Many species, since the modes of their curves lie off the graphs, apparently attain their maximum development on sites not included in this study. If the narrow limitations put upon the choice of stands are recalled, the reasons for this are obvious. These modes could presumably be found by extending the criteria of stand selection to include more mesic prairies on the left (Fig. 3) and cultivated fields and other places where the soil has been recently disturbed on the right.

The causes for the phytosociological behavior patterns of species are to be found in their morphological and physiological characteristics. Neiland and Curtis (1956) listed seven characteristics which appeared directly related to increasing persistence of range and pasture grasses under defoliation: 1) increasing possession of rhizomes, 2) increasing capacity for production of lateral shoots on unclipped plants, 3) decreasing height and erectness of growth habit, 4) increasing lateness of seed germination and spring growth, 5) decreasing growth rate, 6) increasing fertile: sterile stem ratio and 7) increasing lateness of elevation of the stem apex above the minimum point of grazing. The results of the present investigation tend to support the above generalizations. Tall, erect and tussock-forming species such as *Sorghastrum nutans, Andropogon gerardi, and Sporobolus heterolepis* were found to have relatively high positive grazing susceptibility numbers while short-stemmed and rhizomatous species such as *Bouteloua curtipendula, Poa pratensis* and *P. compressa* were found to have negative ones. Similarly, *Andropogon scoparius* and *Muhlenbergia cuspidata* are intermediate in height and rhizome production and were found in the present study to be intermediate in their responses to grazing. The prairie forbs, because they are usually of low forage value, have received comparatively little study and it is not yet possible to

compile a list of the characteristics (as has been done above for the grasses) which determine their behavior under grazing. However, the behavior of some species seems well correlated with such characteristics: *Artemisia frigida* appears unpalatable to livestock because of its aromatic and pubescent leaves; *Erigeron canadensis* and *Verbena stricta* are unpalatable because of their stem and leaf pubescence; while *Taraxacum officinale* and *Plantago major,* because of their low growth form, are inaccessible to grazing animals. If forbs are to be used as indicator species in grazing studies, as has been suggested by Whittaker (1954) and Hanson (1950), their morphological and physiological characteristics are in need of further study.

The origins of the species exhibiting various behavior patterns show that all 48 with positive and 20 of the 30 with negative grazing susceptibility numbers are native prairie plants. No introduced species has a grazing susceptibility number greater than minus 6, indicating that disturbances, however local, must be present before these species are able to become established. That local disturbances are characteristic of native prairie has been pointed out by many authors and is obvious upon a brief visit to a prairie. Burrowing insects, mammals, or other earth movers are constantly working the prairie soil and exposing new materials. It was to such local disturbances that the native weeds (e.g., *Ambrosia artemisiifolia, Erigeron canadensis,* etc.) were once largely confined. With the introduction of domestic livestock, however, disturbed areas were greatly enlarged and introduced weeds from Europe and Asia joined the natives in occupying these new sites. Although the introduced species are relatively few in number they presently dominate large acreages in Wisconsin once occupied by the thin-soil prairies.

Foremost among the introduced species are two bluegrasses—*Poa pratensis* and *P. compressa.* In the present study these species exhibited essentially the same behavior patterns under the influence of grazing. Field observations indicate that they first become established in locally disturbed areas and, once established, produce innumerable stolons and may spread rapidly; the rate of the spread is proportional to the degree of disturbance. The bluegrasses are cool season grasses and produce most of their annual growth before mid-June. Conversely, most of the native prairie grasses scarcely begin growth before mid-June and grow most rapidly during the warm summer months. This difference in growing season permits the bluegrasses to grow with only limited competition from the native plants during the spring months but, unless weakened by grazing, the natives are the better competitors through the summer. There is evidence on these prairies to support the view that the bluegrasses are capable of invading totally ungrazed prairie. They become established on locally disturbed microsites and tenaciously persist long after all evidences of soil disturbances have disappeared. Since local disturbances are frequent in prairies, the accumulated area occupied by the bluegrasses may become considerable and they are sometimes among the dominants of the ungrazed prairie (Table I). The bluegrasses were similarly reported in ungrazed prairies in the Midwest by Weaver and Hansen (1941) and Drew (1947).

It is known that the buffalo severely overgrazed local areas in the Midwest (Roe, 1951). It is suggested that, before the introduction of the bluegrasses onto this continent, recovery from such overgrazing was more rapid than recovery from the same intensity of grazing at the present time. It appears likely that areas overgrazed by buffalo were able to recover quickly since the bluegrasses were not in competition with the prairie plants. In present day bluegrass pastures that have been unused for several years, prairie plants, especially *Bouteloua curtipendula, Andropogon gerardi* and *A. scoparius* begin slowly to recover; the bluegrasses inhibit, but are not able to arrest, their reestablishment and spread.

Spring burning, after the bluegrasses have made considerable growth but before the prairie grasses have begun growth, has been shown to strongly favor the natives when they are in competition with the bluegrasses. Although spring burning is not at present a common practice in this area, it has been used to aid in the reestablishment of prairie on abandoned farmland (Curtis and Partch, 1948). The effects of burning on the thin-soil prairies of Wisconsin have been reported by Dix and Butler (1954).

Of the eight remaining introduced species, all have grazing susceptibility numbers lower than those of the bluegrasses; five are rated as minus 10, indicating the extreme in response to grazing. However, none of these species are confined exclusively to grazed habitats but occur in a wide variety of disturbed areas, such as roadsides, abandoned fields and lawns, throughout the region. This suggests that livestock grazing is not unique but that it shares many characteristics with other types of vegetal and soil disturbances.

A quantitative method for determining the condition of a grazed stand by comparing its species composition with a theoretical climax composition as determined by the use of ungrazed relic areas

has been reported by Dyksterhuis (1949). In this system, the grazed stand is compared with the theoretical climax by adding together the percent cover for all decreasers plus all increasers up to, but not beyond, the cover for these species in the climax. The resulting percentage sum then gives a quantitative measurement of the stand condition which is, in reality, a measure of the residue of the theoretical climax composition which still remains in the grazed stand. Although this system has been successfully used in the classification of range condition on western grazing lands (Parker, 1954), attempts to apply it in the present study proved fruitless because of the highly variable nature of the ungrazed or "climax" prairie stands. An inspection of the graph for *Bouteloua curtipendula* (Fig. 3), for example, shows that the density of this species varied from 1.61 to .12 plants per quadrat in the ungrazed stands, which were all located on similar sites. Thus, in this investigation, the establishment of an idealized climax composition with specific density values assigned to the major species appeared to have little ecological basis. The highly variable nature of the species composition in climax stands has also been demonstrated in other studies which involved the use of large numbers of stands (Hanson and Whitman, 1938; Curtis and McIntosh, 1951; Evanko and Peterson, 1955; Hanson, 1955; and others).

The use of grazing susceptibility numbers appeared in the present study to have two principal advantages over methods which estimate the condition of a grazed stand by measuring the residue of the climax composition remaining in the stand. First, since this method is not dependent upon a theoretical climax composition, the many problems inherent in the establishment of such a composition, as discussed above, were avoided. The second advantage is concerned with the doubtful validity of using the absence or low numbers of a species as an indicator of the ecological character of a stand. In other words, the low numbers or absence of a "decreaser" in a particular grazed stand could not be assumed to be the result of grazing but often appeared due to variations in other factors of the environment or simply to chance. The use of the climax portion remaining in a grazed stand as an index of stand condition attributes all deviation from the climax composition to grazing, while stand condition, as determined by use of grazing susceptibility numbers, is dependent only upon the species present in the stand. The order of stands obtained by use of the grazing susceptibility numbers (Fig. 2) may also be useful as a basis for measuring the "ecological distance" (Whittaker, 1952) between any two stands, grazed or ungrazed, which fall within the framework of the derivation of these index numbers. Presumably, once grazing susceptibility numbers have been determined by the use of paired stands, these numbers may then be used to establish the relative positions of single grazed stands along the grazing ordination.

It may be concluded from the present study that the thin-soil prairies of Wisconsin, as indicated by the phytosociological behavior of their component species, are capable of withstanding moderate, but not abusive, grazing. Although it is not the burden of this investigation to suggest a management program for these prairies, the evidence presented indicates that, if properly mananged, these thin-soil areas might become important sources of auxiliary forage.

Summary

1. The behavior patterns of plant species under the influence of grazing on the thin-soil prairies of Wisconsin were studied by means of paired stands. The stands were selected in such a manner that the only discernible difference between the two members of a pair was grazing. The stands were sampled by the frequency method with at least forty ¼ meter square quadrats used to sample each stand. The frequency data were then converted to densities by employing the well known mathematical relationship between frequency and density. Forty-eight stands (twenty-four partner pairs), located in ten counties, were sampled in this manner.

2. The behavior of species under grazing pressure was determined by comparisons between the densities of the species in the two types of stands. To facilitate this, a formula was developed which when applied would objectively indicate the behavior of each species under the influence of grazing. This formula was used to derive grazing susceptibility numbers for the first 78 species of the study as determined by frequency values. The grazing susceptibility numbers may be thought of as an estimation of the ability of species to withstand the environmental and biotic conditions brought about by livestock grazing. A relatively high plus number indicates that a species is hampered or is at some disadvantage under grazing conditions, while, conversely, a relatively large minus number indicates that a species is benefited by a grazed environment. Grazing susceptibility numbers for some important species are: *Sporobolus heterolepis*, +9; *Sorghastrum nutans*, +9; *Amorpha canescens*, +8; *Andropogon gerardi*, +7; *A. scoparius*, +4; *Solidago rigida*, +1; *Artemisia caudata*, −1; *Bouteloua curtipendula*,

— 4; *Poa pratensis,* — 6; *P. compressa,* — 6; *Euphorbia maculata,* — 9; and *Artemisia frigida,* — 10.

3. The grazing susceptibility numbers were used to weight the relative density values as a means of ordering the stands. This was done by multiplying the relative density value of each species in each stand by its grazing susceptibility number. These figures were then summed to give a single number, the stand index number, which represents the relative position of a stand along the grazing gradient. A stand composed mostly of species with negative grazing susceptibility numbers will have a negative stand index number or, if composed mostly of species with positive numbers, a positive stand index number. The algebraic difference in index numbers between any two stands along the grazing gradient may be thought of as the ecological distance between them.

4. As a means of finding the behavior of individual species along this phytosociological grazing gradient, the densities of each species were plotted against the gradient. Each of these species behavior curves was different although in every case the curves were found to be bell-shaped or some part of such a curve.

5. The deterioration of the native prairies to bluegrass pastures was found to follow a continuous downward curve from climax vegetation.

6. The use of grazing susceptibility numbers to determine stand condition is thought to have certain advantages over methods which estimate stand condition by determinations of the residue of the "climax composition" remaining in a grazed stand. Since this method is not dependent upon a theoretical climax composition, the many problems inherent in establishing such a composition are avoided. In addition, this method is dependent only upon the species present in the stand and therefore avoids the use of the absence or low numbers of a species as indicators of the ecological character of a stand.

References

Anderson, O. 1954. The phytosociology of dry lime prairies of Wisconsin. Ph.D. Thesis. Univ. of Wis.

Archbald, D. 1954. The effect of native legumes on the establishment of prairie grasses. Ph.D. Thesis. Univ. of Wis.

Borchert, J. R. 1950. The climate of the central North American Grassland. Ann. Assoc. Amer. Geographers **40**: 1-39.

Brown, R. T. and J. T. Curtis. 1952. The upland conifer-hardwood forests of northern Wisconsin. Ecological Monog. **22**: 217-234.

Clapham, A. R. 1936. Over-dispersion in grassland communities and the use of statistical methods in plant ecology. Jour. Ecology **24**: 232-251.

Curtis, J. T. 1955. A prairie continuum in Wisconsin. Ecology **36**: 558-566.

——— **and R. P. McIntosh.** 1950. The interrelations of certain analytic and synthetic phytosociological characters. Ecology **31**: 434-455.

——— **and R. P. McIntosh.** 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology **32**: 476-496.

——— **and M. L. Partch.** 1948. Effect of fire on the competition between bluegrass and certain prairie plants. Amer. Midl. Naturalist **39**: 437-443.

Daubenmire, R. F. 1940. Plant succession due to overgrazing in the *Agropyron* Bunchgrass prairie of southeastern Washington. Ecology **21**: 55-64.

Dix, R. L. and J. E. Butler. 1954. The effects of fire on a dry, thin-soil prairie in Wisconsin. Jour. Range Management **7**: 265-268.

Drew, W. B. 1947. Floristic composition of grazed and ungrazed prairie vegetation in northcentral Missouri. Ecology **28**: 26-41.

Dyksterhuis, E. J. 1946. The vegetation of the Fort Worth Prairie. Ecological Monog. **16**: 1-29.

———. 1949. Condition and management of range land. Based on Quantitative Ecology. Jour. Range Management **2**: 104-115.

Ellenberg, H. 1948. Ukrautgesellschaften als Mass für den Sauergrad, die Verdichtung und andere Eigenschaften des Ackerbodens. Ber über Landtechnik **4**: 130-146.

Ellenberg, H. 1950. Landwirtschaftliche Planzensoziologie. I. Unkrautgemeinschaften als Zeiger für Klima und Boden. Stuttgart z. Z. Ludwigsburg: Eugen Ulmer. 141. pp.

Evanko, A. B. and R. A. Peterson. 1955. Comparisons of protected and grazed mountain rangelands in southwestern Montana. Ecology **36**: 71-82.

Fernald, M. L. 1950. Gray's Manual of Botany, 8th Ed. New York: American Book Co.

Fracker, S. B. and H. A. Brischle. 1944. Measuring the local distribution of *Ribes.* Ecology **25**: 283-303.

Goodall, D. W. 1952. Quantitative aspects of plant distribution. Biol. Rev. **27**: 194-245.

Hanson, H. C. 1950. Ecology of the grassland II. Bot. Rev. **166**: 283-360.

———. 1955. Characteristics of the *Stipa comata-Bouteloua gracilis-Bouteloua curtipendula* association of northern Colorado. Ecology **36**: 269-280.

Hanson, H. C. and W. Whitman. 1938. Characteristics of major grassland types in western North Dakota. Ecological Monog. **8**: 57-114.

Hole, F. D., G. H. Robinson, et al. 1952. Soils of Grant County, Wisconsin. Wis. Geol. and Nat. Hist. Surv. and Agr. Exp. Sta. Univ. of Wis.

Launchbaugh, J. L. 1955. Vegetational changes in the San Antonio prairie associated with grazing, retirement from grazing, and abandonment from cultivation. Ecological Monog. **25**: 39-57.

Martin, L. 1932. The physical geography of Wisconsin. Wis. Geol. and Nat. Hist. Surv. Bull. **36**.

Neiland, B. M. and J. T. Curtis. 1956. Differential responses to clipping of six prairie grasses in Wisconsin. Ecology **37**: 355-365.

Parker, K. W. 1954. Application of ecology in the

determination of range condition and trend. Jour. Range Management 7: 14-23.

Raunkiaer, C. 1909. Formationsundersögelse og Formationstatistik. Bot. Tidskr. 30: 20-80.

Robocker, W. C., J. T. Curtis, and H. L. Ahlgren. 1953. Some factors affecting emergence and establishment of native grass seedlings in Wisconsin. Ecology 34: 194-199.

——— **and B. J. Miller.** 1955. Effects of clipping, burning, and competition on establishment and survival of some native grasses in Wisconsin. Jour. Range Management 8: 117-129.

Roe, F. G. 1951. The North American Buffalo: a critical study of the species in its wild state. Toronto: Univ. Toronto Press.

Smith, C. C. 1940. The effect of overgrazing and erosion upon the biota of the mixed-grass prairie of Oklahoma. Ecology 21: 381-397.

Steiger, T. L. 1930. Structure of prairie vegetation. Ecology 11: 170-217.

Transeau, E. N. 1955. The prairie peninsula. Ecology 16: 423-437.

Voight, J. W. and J. E. Weaver. 1951. Range condition classes of native midwestern pastures: an ecological analysis. Ecological Monog. 21: 39-60.

Weaver, J. E. and W. W. Hansen. 1941. Native midwestern pastures—their origin, composition, and degeneration. Nebr. Univ. Conserv. & Soil Surv. Bull. 22: 93 pp.

Whittaker, R. H. 1952. A study of summer foliage insect communities in the Great Smoky Mountains. Ecological Monog. 22: 1-44.

——— 1954. Plant populations and the basis of plant indication. "Angewandte Pflanzensoziologie," Veröffentlichungen des Kärntner Landesinstituts für angewandte Pflanzensoziologie in Klagenfurt, Festschrift Aichinger, Vol. I.

LIMNOLOGY OF SELECTED ARCTIC LAKES IN RELATION TO WATER SUPPLY PROBLEMS[1]

WILLIAM L. BOYD[2]
Arctic Research Laboratory, Point Barrow, Alaska

INTRODUCTION

The flat tundra of the Arctic Coastal Plain of Northern Alaska is characterized by a large number of oriented lakes which may account for less than 25 per cent to as much as 90 per cent of the land's surface, but in most cases make up between 50 and 75 per cent of the surface. These lakes vary from very small tundra ponds to large lakes which may be as much as 9 miles long and 3 miles wide and from a few feet to more than 20 feet in depth (Black and Barksdale 1949).

Since most of the lakes and many of the rivers of the area are free of ice for only a short period during the summer months, the natives rely almost completely on melted ice and snow as a source of water for domestic use during the winter months. In early October, when lake ice is 10-12 inches thick, it is cut and stored for future needs either outside or in cellars which have been dug into the permafrost. Many natives of the coastal areas also make use of "old ice" from the Arctic Ocean for limited supplies of water.

During the summer thaw, all runoff is at the surface since the Arctic Coastal Plain area is underlain for the most part by permafrost (Black and Barksdale 1949). Lakes and rivers sometimes become contaminated by drainage from areas used for the disposal of human and animal wastes. Stefansson (1945) gives an account of an early typhoid epidemic at Barrow, and Pauls (1953) reports that 105 cases with 1 death resulted from an epidemic of bacillary dysentery as recently as 1948. In both cases the source of infection was traced to a contaminated lake which was being used as a summer water source.

Reports of an early expedition (Ray 1885) reveal that the natives of the villages of Nuwuk and Utkia·vik (Uglaamie) in the Barrow area used very little water from October to July because of the lack of fuel with which to melt ice. Even today, it is not difficult to realize why the average per capita consumption of water is only about 2 gallons per day, since it has been estimated that the cost at Barrow of transporting enough ice to yield 100 gallons of water a distance of from 2 to 25 miles is approximately $7.25 (Alter 1950). The present market price for a 55 gallon drum of fresh water (usually available only during the summer months) is $2.50.

With the establishment in recent times of Native Service hospitals, schools, and permanent military establishments, the need for large supplies of water for drinking and boiler purposes has become more urgent. It has been necessary, therefore, to seek out lakes or rivers which do not freeze to the bottom during the winter months

[1] These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and the Arctic Institute of North America. Reproduction in whole or in part is permitted for any purpose of the United States Government.

[2] Present Address: Research Foundation, School of Dentistry, Ohio State University, Columbus 10, Ohio.

and which are near enough to the installation so that relatively large volumes of water can be transported at a minimum of cost. Moreover, since freezing of lake ice tends to concentrate minerals and organic matter in the unfrozen water (Alter 1949), the initial chemical composition of unfrozen lakes has become of primary importance in selecting potential water supply sources.

This study has been carried out on 9 lakes of the Barrow area and other lakes along the Arctic Coast to determine the general potability of selected arctic lakes as well as the magnitude of the seasonal changes in chemical composition which take place.

Methods

All water samples were collected with a sampling rod using chemically clean, sterile sampling bottles. During the winter of 1955-1956, two stations were established on Imikpuk Lake (Fig. 1, lake No. 8), and two samples were obtained at each station weekly by chopping through the ice with an ice chisel. Since little variation was generally observed among the samples, one station was established at this lake and the other lakes under study during the following summer and winter. It was only during the period from the runoff to the time that Imikpuk was ice-free that significant differences among the samples were observed, and, therefore, four samples from different areas of the lake were collected on the given day for sampling each week during June, July, and August. Samples from Imikpuk and other deep lakes were collected at a depth of 8 feet, while water samples at the bottom were obtained from the more shallow lakes.

Selected chemical determinations were carried out on all water samples using Nalco[3] equipment and standard prepared reagents. Total chlorides as NaCl were determined by titration with silver nitrate using potassium chromate as an indicator, total alkalinity as $CaCO_3$ by titration with N/50 sulfuric acid against methyl orange, hydrogen ion concentration colorimetrically using a Taylor slide comparator, iron as Fe by the thioglycollate method, and total and calcium hardness as $CaCO_3$ using a colorimetric titration with Versene (tetrasodium ethylene diamine tetra-acetic acid) with magnesium hardness as $CaCO_3$ being determined by difference. Physical measurements such as air temperature, water temperature, snow cover, and ice thickness were also made at the time of sampling.

Potability tests were performed on five 10 ml portions of each sample using standard methods (A.P.H.A. 1946). All samples were plated in triplicate using nutrient agar (Difco) and then incubated at 37°C for 24 hours prior to counting.

[3] Supplied by National Aluminate Company, Chicago, Illinois.

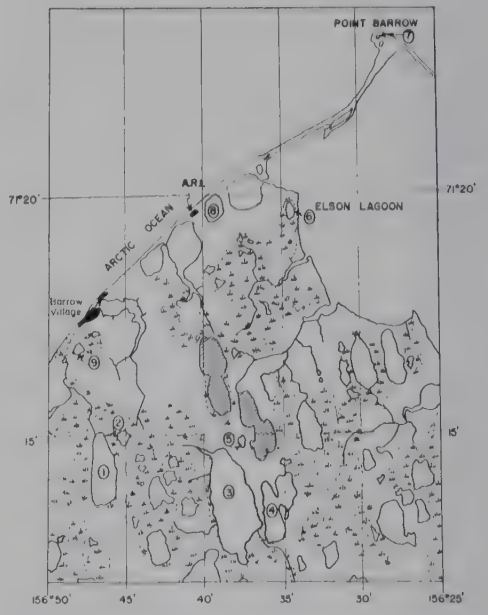


Fig. 1. Sketch-map of the Point Barrow area showing lakes which were sampled.

Results

Several groups of investigators have reported on the limnology of Imikpuk, a coastal lake near the Arctic Research Laboratory at Point Barrow, Alaska (Comita 1956; Comita and Edmondson 1953; Edmondson 1955; and Prescott 1953). This lake was first sampled by the author on January 28, 1956, when the ice cover was 50 inches. The increase in ice thickness during the following months was accompanied by an almost linear increase in the mineral content of the unfrozen water beneath the ice until the maximum ice cover of 79 inches was observed on May 19 (Fig. 2). No iron was present in any of the samples tested throughout this period. The temperature of the water as measured by an alcohol thermometer did not go below 0°C but ranged between +0.5°C and +1.0°C. The lake was covered with snow until June 1 with a maximum snow cover of 9 inches observed on April 6. The pH dropped from a high of 7.3 recorded during January and ranged between 6.7 and 6.9 until July 2 when it rose again to 7.2. Prior to the runoff period, bacterial counts were low (0-26 bacteria per ml), and no coliform organisms were detected in any of the samples collected.

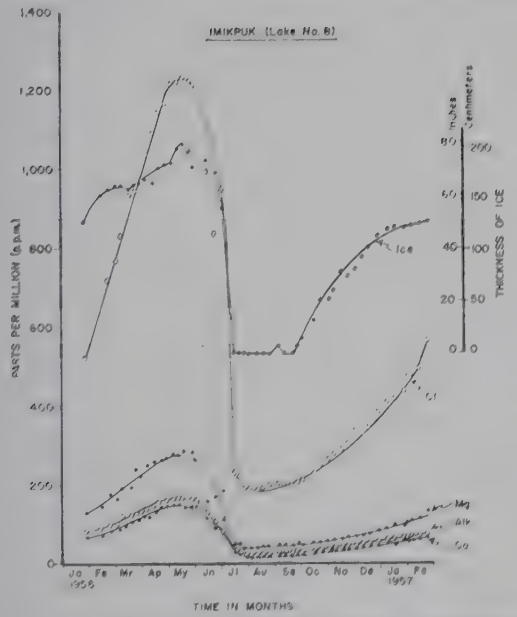


FIG. 2. Seasonal changes in the chemical composition of Imikpuk Lake. Cl = Total chlorides as NaCl; Mg = Magnesium hardness as $CaCO_3$; Ca = Calcium hardness as $CaCO_3$; Alk. = Total alkalinity as $CaCO_3$.

Runoff period

On June 3, the first signs of the summer thaw were evident. During the next two weeks the air temperature rose to as high as $+6°C$, and the snow mantle covering the tundra began to melt rapidly. Since most of this area is underlain by permafrost, downward percolation was inhibited, and a great deal of soil water drained into the lake. The warmer runoff water, running into the lake, caused the melting of the shore ice around its fringes. Concomitant with the melting of the snow, physical changes were also evident in the lake ice which changed from a hard brittle mass to a soft, spongy, candled form which permitted water to diffuse through the ice to a distance of 9 inches from the surface. Small pools of water on the ice were numerous at this time.

On June 19, the ice was still anchored to the bottom at the more shallow parts of the lake and had melted to a distance of approximately 4 feet from the shore. It was during this period that samples taken from different parts of the lake showed the greatest variation in chemical composition. Bacterial counts of samples taken from the main part of the lake were low (6-18 bacteria per ml), although all samples taken from the ice-free fringe had counts of greater than 300 bacteria per ml. While the mineral content in the main body of the lake began to decrease slowly, water from the open areas which was composed of melted lake ice mixed with runoff water presented a mixture which was of far lower mineral content than the main body of the lake.

During the greater part of the thaw period chemical and bacteriological studies were carried out on samples of runoff water. Although no quantitative bacterial counts were performed, potability tests were carried out on all samples. Two general areas were studied. The lake is bordered on the west by a series of gravel beds which have a soil pH of 6.0 to 6.5 and on the south by a more acid flat area (soil pH 5.4 to 5.8) consisting of peaty tundra soil. In general, the water from the gravel area was clouded by colloidal mud, while the runoff from the tundra area was clear but amber in color due to the presence of various humic acids. The chemical composition of these samples, while variable, was, nevertheless, of lower mineral content than the water still under the ice and resembled more closely the water found around the margin of the lake.

Twenty-nine samples were analyzed, 9 from the gravel beds and 20 from the tundra area. Coliform organisms were isolated from 31 per cent of the samples. In all probability, many intestinal organisms were leached from lemming pellets which were quite numerous on the tundra area adjacent to the lake. Moreover, a sled trail to a whaling camp crossed the lake, and dog feces were probably the source of some of the coliform organisms found in the water.

By July 14, the ice was free-floating and subject to shifting and breaking due to wind action. On July 28, the lake was completely free of ice as were all coastal lakes from Point Barrow to the Colville River observed on August 7, with the exception of Teshekpuk Lake which still had a small quantity of slush ice pushed into the northeast corner.

Ice-free period

After all the ice had melted, the mineral content of Imikpuk was at its lowest, and samples taken from all parts of the lake were potable. It was only once, on September 13, that *Escherichia coli* was found to be present in all the samples collected. During this period the large number of arctic foxes, which were present around the lake, ventured out on the thin ice which formed and melted periodically. Whenever animals in any numbers were present around a particular body of fresh water, coliform organisms were always observed to be present in the samples collected. This was especially true for a small stream south of Point Lay and several lakes east of the Colville River which were sampled shortly after a herd of

TABLE I. Bacterial and chemical composition of selected arctic lakes during the ice-free period.

Date	Location	Chloride (NaCl)	Calcium hardness ($CaCO_3$)	Magnesium hardness ($CaCO_3$)	Total alkalinity ($CaCO_3$)	Iron (Fe)	pH	Temperature (°C)		Maximum depth in inches	Bacteria per ml
								air	water		
		p. p. m.									
8- 7-56	Pitt Point	100.6	32.2	33.3	41.7	1.5	7.6	5	6	28	12
8- 7-56	Cape Simpson	333.7	42.2	64.3	15.4	1.0	7.1	6	4	28	29
8-21-56	Point Lay	46.2	31.3	29.8	50.8	1.0	7.6	2	5	96	13
8-21-56	Wainwright	26.2	16.0	8.4	16.3	2.0	7.3	0	2	48	68
8-31-56	Barter Island	140.2	61.9	42.7	56.2	0.0	7.7	3	2	90	0
	Point Barrow										
9-13-56	Lake #6	381.8	47.8	88.6	18.2	0.0	7.3	1	3	39	46
9-13-56	Lake #7	232.2	32.2	92.2	86.8	0.5	8.2	2	3	40	88
9-13-56	Lake #8	200.8	23.4	44.8	28.6	0.0	7.4	1	3	108	8
9-14-56	Lake #1	32.2	12.2	12.0	12.6	0.0	7.2	1	2	54	0
9-14-56	Lake #2	92.4	44.0	24.2	32.6	1.5	7.4	1	2	19	0
9-14-56	Lake #3	46.2	8.2	9.8	6.4	0.5	7.2	1	3	80	3
9-14-56	Lake #4	42.6	14.2	10.0	12.2	1.5	7.2	2	3	51	1
9-14-56	Lake #5	68.2	14.2	18.1	8.6	1.5	7.2	1	4	28	6
9-14-56	Lake #9	97.0	31.4	33.8	29.0	3.0	7.3	1	3	29	2

caribou had passed through. In all cases, the period in which coliforms could be detected was short, suggesting that the environmental conditions of arctic lakes are adverse to the survival of coliform organisms for long periods.

In addition to Imikpuk, 8 other lakes of the Point Barrow area and selected lakes of the Arctic Coast were sampled during the ice-free period. From the results presented in Table I, it can be seen that wide variations in chemical composition were observed in most of the lakes studied. These data further emphasize that lakes of the same general type and in close proximity to one another may differ chemically and also in the numbers of bacteria present. These results confirm the observations of Prescott (1952) who reported differences in the algal flora and chemical composition of lakes in the Point Barrow area.

Freeze-up period

The first signs of the approaching freeze-up were observed on August 23 when one-fourth of Imikpuk Lake was covered with a thin film of ice. During the following month, the lake periodically froze and thawed until a permanent ice cover of 3 inches was recorded on September 27. Concomitant with the frequent periods of freezing and thawing, rapid fluctuations in water temperature occurred with as much as a 4°C change being observed in one day.

Prior to the freeze-up, two other lakes and a small pond in the Point Barrow area were sounded and sampled. In addition to Imikpuk, these more shallow bodies of water were studied during the fall until they froze to the bottom. The lake at Brant Point (Fig. 1, No. 6) was 39 inches deep, while the lake south of Barrow was more shallow with a maximum depth of 29 inches (Fig. 1, No. 9). The small pond at Nuwuk (Fig. 1, No. 7), formed by drainage from high gravel beds which border Elson Lagoon, and located on the sandy beach close to the Arctic Ocean, was 40 inches in its deepest part.

The data plotted in Fig. 3 are typical for the two tundra lakes. The rate of concentration of minerals in water under the ice is accelerated as the ice approaches the lake bottoms since they are underlain with permafrost which effectively makes the lake basins a closed system. The linear increase in mineral content for the pond at Nuwuk (Fig. 4) is interesting and is probably due to the absence of permafrost immediately beneath the pond, which would allow minerals and organic matter to seep into the porous gravel bottom. During the same period, Imikpuk, which is much larger and deeper than the Nuwuk pond showed a similar rate of increase in mineral content (Fig. 2). The Imikpuk data for early 1957 generally agree well with the data from 1956 even though the ice was thinner in 1957 due to a greater snow cover and warmer winter.

DISCUSSION

During the past decade great interest has been focused on the far North because of the present world political situation and as a possible future area for colonization to take care of the world's increasing population. As more people emigrate to the polar regions, a knowledge of the physical and biological environment of this area will become more important to meet the daily requirements of living under extremely cold conditions. Water treatment practices carried out in warmer

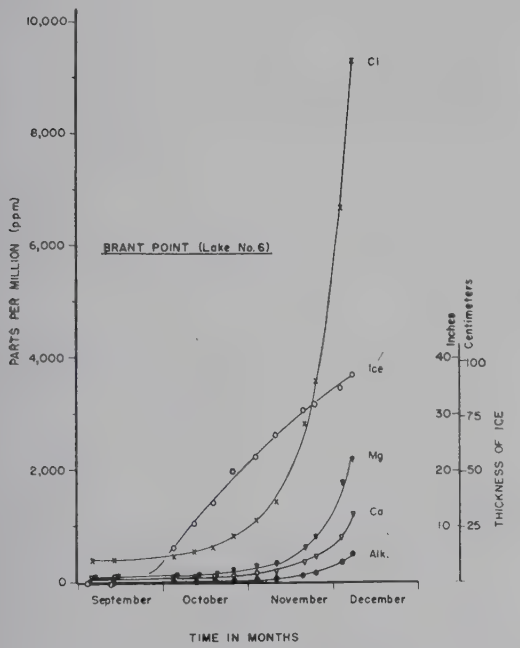


FIG. 3. Changes in the chemical composition of a lake at Brant Point prior to freezing to the bottom. Legend as presented for Fig. 2.

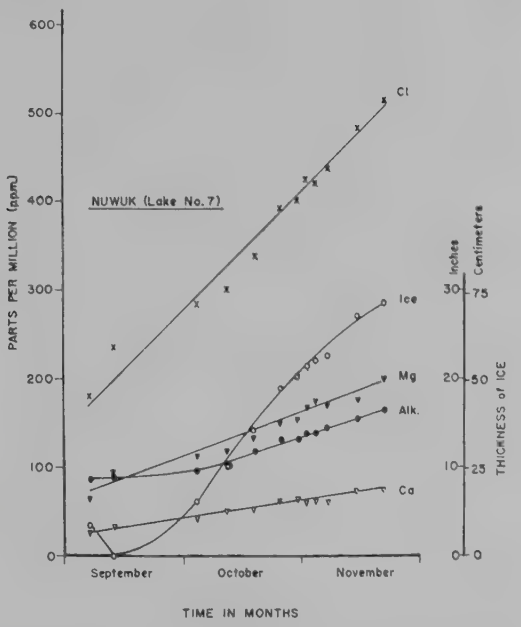


FIG. 4. Changes in the chemical composition of a pond at Nuwuk prior to freezing to the bottom. Legend as presented for Fig. 2.

regions will have to be modified to meet the requirements imposed by the arctic environment.

From the limited data presented it can be assumed that water pollution for most of the year is not a serious problem except during and shortly after the runoff period, especially in areas where human and animal waste might be carried into the water. Organisms capable of growth at 37°C are low in numbers except in parts of a lake which have been contaminated by soil runoff water; coliform organisms do not remain viable in arctic lake water for long periods of time. However, public health control measures for water purification are as necessary as they are in temperate areas.

Since minerals are concentrated in the unfrozen water of arctic lakes as the ice cover increases, care must be exercised in selecting a lake as a source of water. While a lake might be low in chlorides, hardness, and other minerals during the ice-free period, it may be necessary to carry out extensive water treatment during the season when the lake ice increases in thickness. Cost of chemicals for water treatment will be expensive since many settlements in arctic regions can only be reached by airplane. Until cheaper methods of water treatment are perfected, cost will probably determine the type and extent of water treatment used and may also play a role in determining the number of people who will be able to settle successfully in a given area.

SUMMARY

The chemical composition of arctic lake water changes with increased ice cover as would be expected. Any type of water treatment for either drinking or boiler purposes must be varied to meet the marked seasonal changes in the quality of the water. A suitable lake should be over 8 feet in depth, for the greater the depth, the less concentration occurs. A low mineral content during the ice-free period is one of the more important criteria in the selection of a potential water supply. Small lakes can be used as temporary summer and early fall sources, but the quality of water becomes progressively poorer, especially as the ice approaches the bottom of the lake.

In general, most of the lakes studied were potable and could serve as a satisfactory water supply, except during and shortly after the runoff period when contamination from soil water occurred. From the data presented, it seems reasonable to assume that coliform organisms do not survive for long periods in arctic lake water.

REFERENCES

Alter, A. J. 1949. Water supply problems of the Arctic. Alaska's Health. **7**: (3).

———. 1950. Water supply in Alaska. Jour. American Water Works Assoc. **42**: 519-32.

American Public Health Association. 1946. Standard methods for the examination of water and sewage. 9th ed. 286 pp. New York.

Black, R. F. and W. L. Barksdale. 1949. Oriented lakes of northern Alaska. Jour. Geol. **57**: 105-18.

Comita, G. W. 1956. A study of a calanoid copepod population in an arctic lake. Ecology **37**: 576-91.

——— **and W. T. Edmondson.** 1953. Some aspects of the limnology of an arctic lake. Stanford Univ. Pub., Univ. Ser. Biol. Sci. **11**: 7-13.

Edmondson, W. T. 1955. The seasonal life history of Daphnia in an arctic lake. Ecology **36**: 439-55.

Pauls, F. P. 1953. Enteric diseases in Alaska. Arctic **3**: 205-12.

Prescott, G. W. 1953. Preliminary notes on the ecology of freshwater algae in the arctic slope, Alaska, with descriptions of some new species. Amer. Midl. Nat. **50**: 463-73.

Ray, P. H. 1885. Report of the international polar expedition to Point Barrow, Alaska. Washington: Government Printing Office. 695 pp.

Stefansson, Vilhajalmur. 1945. Arctic manual. New York: Macmillan. 556 pp.

OBSERVATIONS ON THE AUTECOLOGY OF *HYPERICUM PERFORATUM*[1]

E. W. Tisdale, M. Hironaka and W. L. Pringle[2]
Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, Idaho

Introduction

One of the most striking ecological phenomena occurring on western range lands during the past few decades has been the introduction and subsequent rapid increase and spread of weedy species. A prime example of such an invader is *Hypericum perforatum* L. (St. Johnswort, Klamath weed or goatweed). During the past four or five decades this introduced perennial forb has become a major weed on ranges in the Pacific Northwest and California. Prior to the advent of biological control, the area infested by this species in California was estimated at 400,000 acres (Huffaker and Holloway 1949). The total area infested in the Columbia Basin region was recently estimated at 1,217,000 acres (Columbia Basin Noxious Weed Control Task Force 1952). The estimated acreage by states was as follows: Oregon 370,000 acres; Washington 122,000 acres; Idaho 615,000 acres; and Montana 115,000 acres. In Montana where the weed was introduced more recently than in the other states, the estimated area of infestation had increased to 211,000 acres by 1956 (Morris and Meuchel 1956). In Australia the plant has been a major range weed for a considerable period (Wilson 1943).

A native of southern Europe, *Hypericum perforatum* was reported from the northeastern United States as early as 1793 (Sampson and Parker 1930). The date of its entry into the Pacific coast states is unknown, but the first reported collection known to the authors is that of W. N. Suksdorf in Clackamas County, Oregon in 1893 (Pringle 1952). The plant appears to have reached northern California about 1900. As late as 1906 it was reported still relatively local in occurrence in Washington (Piper 1906). The spread of the weed into Idaho evidently occurred somewhat later, but by 1930 it had become sufficiently abundant in parts of the upper Clearwater and lower Salmon drainages to cause concern. During the next 20 years, St. Johnswort invaded a major portion of the grasslands of north central Idaho, as well as considerable amounts of open or cut-over forest land. Observations by persons living in the area during this period indicate the rapidity of increase. Evans (1952) reports that *Hypericum perforatum* was absent or rare in Nez Perce County in the northern part of the state as late as 1936. By 1948 the infestation was so heavy that some of the initial releases of *Chrysolina* beetles for biological control in Idaho were made in this county.

St. Johnswort is undesirable on range lands for two reasons: first, as an aggressive species of low livestock preference, and second because of its toxic properties. Heavy grazing tends to favor *Hypericum* at the expense of more palatable species and the presence of significant amounts of the weed on a range area lowers the grazing capacity. The toxic properties are due to the presence of two substances, hypericin and hypericum red contained in the leaves and flowers which are capable of causing poisoning by photosensitization (Muenscher 1951). Death due to the consumption of the plant is rare, but serious losses in weight and condition of livestock have been reported by Marsh and Clawson (1930). The major role of *Hypericum perforatum* on range lands appears to be that of an aggressive range weed rather than a poisonous species.

The present paper reports the data obtained from studies on the autecology of *Hypericum perforatum* made during the period 1951 through

[1] This work was supported by a grant from the Special Research fund of the University of Idaho.

[2] Presently Agronomist, Canada Range Experiment Station, Kamloops, B. C., Canada.

1955 in northern Idaho. The Range Management staff of the Forest, Wildlife and Range Experiment Station of the University of Idaho conducted this work as part of a project on the ecology of *Hypericum* and its control by insects. This project was carried on cooperatively with the Departments of Entomology and Agronomy of the Agricultural Experiment Station. Data regarding the effects of *Chrysolina* and other insects on *Hypericum,* and the changes in vegetational cover resulting from this biotic pressure will be presented in a subsequent paper.

No attempt was made in this project to conduct a comprehensive study of the autecology of *Hypericum.* Instead, a few features thought to be of special significance were selected for investigation. These included the plant's sexual and vegetative reproduction, root development and phenology.

Detailed taxonomic descriptions of *Hypericum perforatum* are given by Sampson and Parker (1930) and Pringle (1952). Most of the literature on the ecology of the plant is concerned with its control by biological or other means, with the autecology of the plant a minor consideration. The few autecological references which were found are discussed in the sections of the text where they are pertinent rather than in a formal literature review.

Specimens of *Hypericum perforatum* were collected at several sites in order to document the type of material occurring in the study area. These vouchers are deposited in the Range Management Herbarium of the College of Forestry at the University.

Description of the Study Area

The studies described were all conducted in that portion of Idaho lying north of the Salmon River, since it is in this region that virtually the entire *Hypericum perforatum* infestation of the state occurs. Within this general area this species occurs on a wide variety of habitats and appears well adapted to the existing climatic and soil conditions.

The southwestern portion of the area belongs to the Columbia Plateau, formed by Columbia River basalt of the Miocene period, with much of it subsequently covered by a mantle of loessial material. This rolling plateau varies in elevation from 2400 to 3600 feet above sea level and is deeply dissected by the valleys of the Clearwater, Snake and Salmon Rivers. The sides of these valleys and their tributaries are characterized by large areas of steeply sloping land on which slopes of 30 to 60% are common. To the north, east and south the area is occupied by mountains of granitic origin. The extreme northern portion was glaciated during the Pleistocene and has valley bottoms covered with deposits of glacial till and outwash materials.

The climate is characterized by the Pacific coast type of seasonal precipitation, with over half of the annual total occurring from October through April. Precipitation during July and August is normally very low. Temperatures are relatively mild for the latitude, especially in the lower valleys. Data for a few representative stations in the study area are presented in Table I.

Table I. Climatological data for representative stations in *Hypericum*-infested portions of northern Idaho

Station	Elevation (feet)	Latitude	Mean Precipitation (inches)		Mean Monthly Temp. (F.)	
			Annual	Oct.-March	July	January
Coeur d'Alene	2273	47°46′	24.35	16.6	69.1	27.1
Moscow	2628	46°44′	21.70	14.7	67.2	28.2
Lewiston	743	46°25′	13.98	7.7	76.1	33.2
Grangeville	3409	45°56′	23.60	11.9	67.7	28.6
Riggins	1685	45°25′	14.25	7.6	76.6	34.3

The soils of the area have received considerable study in the cultivated sections but only preliminary data are available for the forest and range areas (Fosberg 1956). The forest soils belong primarily to the Brown Podzolic great soil group with some Western Brown Forest and Grey Wooded soils in localized areas. The parent material of the forest soils is derived mainly from residual material from the Idaho batholith and the metamorphic Belt Series.

The grassland soils include the Prairie, Chernozem and Chestnut zones. Most of the area occupied by the Prairie soils is under cultivation and this is also true of the Chernozem except where the topography is very steep. The existing grassland areas occur largely in the Chestnut zone. The Prairie and Chernozem soils have developed on both loess and residual basalt, the Chestnut soils mainly on residual materials. In spite of the steep topography over much of the study area, the soils are relatively deep, with solum depths ranging from 30 to 42 inches on most sites. Rock fragments are found commonly throughout those profiles derived from residual materials. The texture of the A horizon on most of the sites is a loam or silt loam. The pH of the A horizon varies from 6.1 to 6.8, and the organic matter varies from 4.5 to 8.4 percent.

The vegetation includes a number of forest and grassland communities. *Pinus ponderosa, Pseudotsuga, Thuja/Tsuga* and *Picea/Abies* zones comprise the forest vegetation (Daubenmire 1952).

These forests cover the greater portion of the northern part of the state.

The grasslands are limited primarily to areas in or adjacent to the major river valleys. The vegetation resembles that described by Daubenmire (1942) in eastern Washington and adjacent Idaho, but no detailed study has been made yet of the grasslands in Idaho south of the Clearwater River. Two principal zones, the *Festuca/Agropyron* and *Agropyron/Poa* can be distinguished. The former is associated with soils of the Chernozem and Prairie great soil groups, and the latter zone with Chestnut soils. Due to cultivation of the more mesic areas, the bulk of the remaining grasslands are in the *Agropyron/Poa* zone.

The spread of *Hypericum perforatum* into northern Idaho has resulted in the establishment of this species in several vegetation zones and under a variety of topographic and soil conditions. The largest areas of infestation have been in the grassland zones along the main valleys and lower tributaries of the Clearwater, Salmon and Snake Rivers. By 1950, large areas in the grassland zones were supporting medium to dense stands of *Hypericum* (Fig. 1). The occupation by this species was facilitated greatly by the depleted condition of these grasslands, on which the perennial climax dominants had been largely replaced by annual grasses (chiefly *Bromus* spp.) and annual forbs.

FIG. 1. Dense *Hypericum perforatum* infestation in Whitebird Creek area of northern Idaho. The annual vegetation has been replaced largely by the aggressive weed.

In forested zones the spread of *Hypericum* has been confined mainly to naturally open forest stands or to areas where the tree cover has been greatly reduced by logging, fire or other disturbance. Hence, its main area of establishment has been in the more open portions of the *Pinus ponderosa* zone and in cut and burned over areas in all of the forest zones listed previously. While the resulting distribution of *Hypericum* is wide, the areas where it is abundant are localized and much less extensive than those which developed on the grasslands. No significant spread of *Hypericum* into well-stocked forest stands has been observed in any of the zones except the ponderosa pine.

EXPERIMENTAL RESULTS

Seed production

Field observations indicated abundant seed production by *Hypericum perforatum* at all sites each year of the study, except from plants killed or seriously weakened by the feeding of *Chrysolina* beetles. In view of the apparently nonlimiting nature of seed production, no elaborate studies of this factor were considered necessary. Some seed production data were obtained, however, in the course of other work. During the years 1952 and 1953, the number of stalks per plant was determined for a total of 512 plants growing at six sites selected to represent the range conditions within the *Agropyron/Poa* zone on the Clearwater River. From this population, the number of seed capsules was determined on 92 stalks, and the number of seeds counted in 21 capsules. The means obtained were 69 ± 9.8 seeds per capsule, 94 ± 12.2 capsules per stalk and 3.6 ± 0.4 flower stalks per plant. The average seed production was 23,350 seeds per plant. This agrees reasonably well with Salisbury's (1942) estimate of 26,000 to 34,000 seeds per plant per year in England, and Sampson and Parker's (1930) "conservative estimate" of 15,000 in California.

Great variability in amounts of seed per plant was observed in the field, with individual production varying from a few thousand to nearly 100,000 seeds. In addition to site factors and seasonal growth conditions, intraspecific competition appeared to be involved. No direct tests of this latter factor were made, but Evanko (1953) in northeastern Washington found the number of seeds per plant to be much greater in peripheral than in centrally located individuals in dense stands of *Hypericum*.

The small and somewhat sticky seeds of *Hypericum* have no devices to facilitate dispersal by wind or direct plant action and it has been generally assumed that animal or water transport are the main factors involved in such dispersal (Harris 1951). A few tests conducted during the course of the present project indicate that wind cannot be ignored as a dispersal agent. Series of cloth-bottomed seed traps each measuring 18 by 18 inches were distributed 10, 20 and 30 feet

respectively down wind from the nearest *Hypericum plants*. During the period September 15 to October 30, during which most of the *Hypericum* seed at these sites was shed, an average of 148, 27 and 7 seeds were caught in these traps. From these results it appears that the movement of *Hypericum* seed by wind may constitute a significant factor in the local spread of the species, aided of course by vegetative propagation.

Seed germination

Germination trials in the laboratory were conducted with seed lots representing different sites, years and seasonal dates of collection. All samples had been stored at room temperature. For each lot tested quadruplicate samples of 100 seeds each were placed on commercial seed blotters in Petri dishes and kept moist with distilled water. Temperatures in the germination room ranged from 70 to 78 degrees Fahrenheit during the 24-hour cycle. The results of a few of these trials are summarized in Table II.

TABLE II. Laboratory germination of filled *Hypericum perforatum* seed collected in different years and from different sites

Source and date collected	Percentage germination, Feb. 1953. (21 days)
Colville, Washington 1950	96.0
Unknown 1937	50.2
Site #2, Clearwater Bench, Idaho 1951	36.2
Site #9, Salmon River Bench, Idaho 1951	84.2
Site #10, Salmon River, Idaho 1951	72.3
Site #10, Salmon River, Idaho 1952	58.3

The results indicate large differences in germination among sites in collections of the same year. Striking retention of viability in seed stored under room conditions is evident also. The average germination for all mature seed lots tested, including many lots not included in Table II, was 65 percent.

A few tests were made to determine viability of newly ripened seed. In the fall of 1953 seed collections were made from one site at approximately one week intervals from mid-September to mid-October and each lot was tested for germination within 3 to 6 days of the collection date. Only seed that appeared ripe was used in these tests. Forty-three percent germination was obtained from the samples collected earliest, but those collected later showed some increase, reaching a maximum of 58 percent germination. These samples required 2 to 5 days longer to start germination than did the lots reported in Table II where the minimum interval between collection and testing was 3 to 4 months.

These findings are somewhat at variance with those of Cashmore (1939) in Australia, who reported the need for a period of several months after seed maturity before any significant amount of germination occurred. Sampson and Parker (1930) in California reported germination percentages varying from 5.5 to 63.5 percent for duplicate seed lots tested over a 40-day period in sterilized sand in the greenhouse. No indication of the age of the seed or of the period elapsed since ripening was given. The same workers reported a definite stimulation of germination from immersion in water for 5 to 20 days. Increased germination was also obtained by brief exposure of dry seed to temperatures of 212 and 260 degrees Fahrenheit. Germination percentages up to a maximum of 74 percent with water immersion and 81 percent with heat treatments were obtained. Germination of the normally treated check lots averaged only 44 per cent.

Cashmore was working with *H. perforatum* var. *angustifolia* the seed of which shows considerable dormancy due to an exudate of the leaves and seed capsules (Clark 1952). The California material does not appear to belong to the var *angustifolia,* although the reaction to water immersion and to heat treatments suggests the possibility of a similar inhibiting factor.

From the Idaho results, it would appear possible for *Hypericum* seed to germinate in the field in the same season that it is produced. In actual practice, this phenomenon was not observed during the course of the study, nor does it appear to have been reported elsewhere in North America. In Idaho and adjacent areas, the explanation may lie in the relatively low soil temperatures which normally occur during the period (October-November), when soil moisture conditions are likely to be adequate for germination. Studies by Clark (1953) in Australia indicate that field germination of *Hypericum* did not occur when mean "screen" temperatures were below 52 degrees F., and most germination occurred at much higher temperatures.

Seed longevity

Retention of viability by *Hypericum* seed under room storage conditions over a long period of time has been reported by many workers and is illustrated by the results obtained in the present study (see Table II). A more important point is the length of time during which viability may be retained under field conditions. In Australia, Clark (1953) found that *Hypericum* seeds may

remain viable in the soil for as long as 6 years. According to Clark's studies, germination is inhibited by an exudate of the seed capsules and to a lesser extent of the leaves, as well as by unsuitable moisture or temperature conditions. Bellue (1945) cites 10 years as the period over which *Hypericum* seed can retain viability in the soil under California conditions.

In the present study, the viability of buried seed was tested over a 3-year period. Lots of 100 seeds each were placed in baskets of 100-mesh brass screen measuring 1 by ¼ by ¼ inches and buried in silt loam soil at depths of ½, 1 and 3 inches, in unglazed clay pots. These pots were set in the ground so that their tops were level with the soil surface. Three replicates of seed were used for each depth in each year. The study site was located near Lewiston, Idaho at an elevation of 1400 feet in the *Agropyron/Poa* zone, with annual precipitation of about 14 inches.

After removal from the pots, the seeds were recovered from the baskets with the aid of a fine jet of water and a low-power binocular microscope. Ninety to 95 percent of the seeds were recovered in this manner, and tested for germination by the method described earlier. The results are presented in Table III.

TABLE III. Laboratory germination of *Hypericum perforatum* seed recovered after burial in soil at 3 depths for periods of 1 to 3 years

No. years buried	GERMINATION IN PERCENT[1]		
	½-inch depth	1-inch depth	3-inch depth
1	20.6	27.3	25.2
2	30.6	42.0	62.0
3	9.6	45.0	52.0

[1]Germination percentage is calculated on basis of 100 seeds originally buried in each lot.

The results indicate that a considerable proportion of *Hypericum* seed may be expected to retain viability for at least 3 years, particularly if buried to a depth of 1 inch or deeper. The seeds stored at the ½ inch depth showed the greatest amount of disintegration, while those at greater depths appeared little affected even after 3 years. Only limited germination occurred in the field from this buried seed. During the first year the germination rate was 9 percent for the seed buried at ½ inch, 5 percent at 1 inch and only 1 percent for the seed at 3 inches. A few of the seedlings from the ½-inch depth emerged at the soil surface, although none survived. There was no emergence from the 1-inch and 3-inch depths. Probably the minute amount of stored food present in the small seeds of *Hypericum* is not sufficient for emergence of seeds buried much deeper than ½ inch in the soil.

The fact that *Hypericum* seed retains viability for several years in the soil is significant in relation to the ability of this species to reoccupy a site on which the living plants of this species have been removed as a result of biological or other control measures. The combination of a high rate of seed production and longevity of seed results in a situation whereby any site which has supported a stand of *Hypericum* for even a few years has a high potential for seedling production for several years after the stand is removed.

Reproduction studies

Seedling development and survival in the field was studied at 3 sites in 1952 and 8 sites in 1953. These areas constituted a cross-section of the study area with respect to vegetation and habitat. At each site 3 permanently marked sample plots each 2 by 5 decimeters in size were established on areas where *Hypericum* seedlings could be found in significant numbers. At all sites there was a well-developed cover of older plants of *Hypericum*, along with other annual and perennial grasses and forbs.

Several times during each year, records were made of the number of seedlings present in the sample plots, and their subsequent development and fate. It was found that seed germination occurred principally in early May, at a time when soil moisture was normally in good supply and temperatures favorable for plant growth. The number of seedlings per sample plot averaged 57 in 1952 and 71 in 1953. Considerable differences in number of seedlings per site occurred in a few cases, but these did not have any obvious relationship to vegetation or habitat. Seedling mortality was extremely high both years, averaging 96 percent in 1952 and 99 percent in 1953. The critical period for seedling survival came in late July and in August. Normal precipitation for these two months is low at the sites studied, amounting in most cases to less than one inch total for the 2 months. Air and surface soil temperatures are at their maximum for the year during this same period.

Comparisons of climatic data for 1952 and 1953 with the long-term means were made at several stations located close to certain of the seedling study sites. The data indicate that total precipitation was not far from normal in either year. In 1952, precipitation during June was above normal at all stations, but was below normal in July and August. In 1953, June precipitation was close to normal, while that for July was below and for August above normal. The August rains arrived

too late to aid the seedlings. In both years the accumulated precipitation from the previous October through August of the test year was close to normal.

The severity of the soil moisture deficiency normally resulting from plant use combined with minimal summer precipitation was evident from the results of soil moisture studies on these and other comparable sites. In 1951 the moisture content of the surface foot of soil at 10 representative sites remained almost continuously at or below the wilting point (determined directly by plants grown in the greenhouse) from early July through mid-September. In 1953, a study of 4 sites, 2 in the Clearwater and 2 in the Salmon River drainage, gave similar results. Soil moisture in the surface foot was close to or at the wilting point by July 10, and by mid-August no available moisture remained in the upper 18 inches of soil.

Under these circumstances, it is evident why most seedlings failed to survive. Sampson and Parker (1930) reported a similar situation in *Hypericum*-infested areas of northern California. These authors found that in most years, seedling survival was practically nil, but that the occurrence of more favorable moisture conditions resulted in an enormous spread from seed in occasional years. The pattern of *Hypericum* distribution in Idaho suggests a similar situation in which many small patches enlarge slowly by vegetative means, and then occasionally expand rapidly through seedling production to coalesce and cover large areas.

Seedlings which did survive the summer drought attained a height of 2 to 4 inches above ground and extended their roots to a depth of one foot or more. Some additional mortality of seedlings during their first winter was observed, especially on sites where snow cover was deficient.

Vegetative reproduction of *Hypericum* by crown or root sprouts has been reported by many workers, and in Australia some layering has been observed (Clark 1953). Observations made during the present study indicated that vegetative propagation was stimulated when *Hypericum* plants were affected by grazing, fire, defoliation (if not too severe) and the presence of shallow or very rocky soils. Clark reported similar reactions of *Hypericum* in Australia and stressed the relation of poor site quality to increased vegetative propagation.

In the field, it was observed that vegetative spread was due mainly to sprouting of lateral roots a few inches below the soil surface (Figure 2). In greenhouse experiments, sections of root sprouted when buried at depths up to 2 inches in moist silt loam soil, but failed to sprout at greater depths. On the 4-inch root sections used, 2 sprouts sometimes developed.

FIG. 2. Vegetative propagation by root offshoots in *Hypericum perforatum*. The linkage deteriorates by the time the new plant is a few years old.

In general, plants propagated vegetatively were found to sever connections with the parent plant fairly soon after the new plants became established. This made it difficult to distinguish crowns developed by vegetative means from those arising as seedlings. It was noted, however, that plants which developed from seed formed tap-roots whose axes were in a straight line with their crowns. The tap-roots of vegetatively propagated plants invariably were not so aligned. Using this criterion of difference, a check was made on 6 sites to determine the proportion of crowns established by the 2 modes of propagation. Counts of 208 crowns indicated that 46 percent had arisen by vegetative means. It is probable that an even higher percentage of asexual spread would have been found on denser stands and poorer sites than those examined.

Root studies

The root system of *Hypericum* was studied to a limited extent. The main objective was to determine how the root system compared with those of competing plants, especially some of the native perennial grasses. Altogether, 8 root systems of *Hypericum* were examined by means of the trench method (Weaver 1919). Roots were exposed on

the vertical face of a 2 to 5 foot trench by picking at the soil with a sharp-pointed tool. Grid lines were used to aid in sketching the exposed roots (Figure 3).

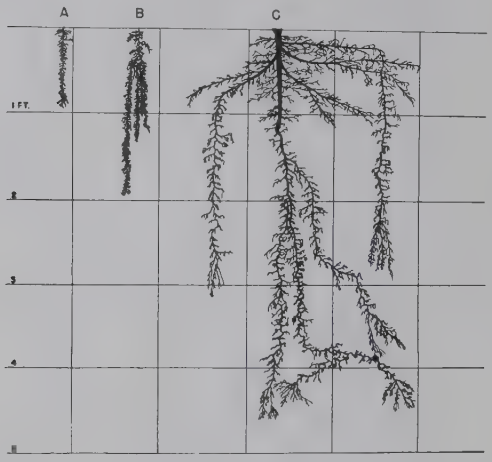


FIG. 3. Sketches of root systems of *Hypericum perforatum* plants exposed by trench method. A. 6-month-old plant. B. 17 months. C. Mature plant 3 or more years of age.

It was found that extensive root development was present in seedlings and 1-year old plants of *Hypericum,* even while top growth was still relatively small. Conspicuous branching of the root system began in the second growing season. The roots of mature plants were found to depths of 4 to 5 feet where soil depth permitted. Extensive lateral roots which developed a few inches below the ground surface functioned in vegetative propagation. Studies of soil moisture made at various times indicated that the root system of *Hypericum* functions well for water absorption at considerable depths. As indicated in the data on seedling mortality presented earlier in this paper, the normal march of soil moisture in the study region involves drought to increasing depths as the season progresses. The moisture situation on most of the study sites closely resembled that reported by Daubenmire (1942) for the *Agropyron/Poa* zone in eastern Washington.

On the study sites, soil moisture was almost always reduced to the wilting point (10-14 percent) down to the 12 or 18 inch depth by early July, at a time when the *Hypericum* plants were still in bloom and when most of their foliage was still green. In several cases, the plants remained green and apparently well supplied with moisture for periods of 2 to 4 weeks during which no available moisture was present above the 24-inch depth. In a one-season study of plant-soil moisture relationships Harshman (1956) found that reduction of the moisture content of *Hypericum* plants from their early summer average of 60 percent or more did not occur until soil moisture at the 24 to 30 inch depth was depleted below the wilting point.

It is evident from these observations that the root system of *Hypericum* is well adapted to enable the plant to compete on grasslands or open forest in northern Idaho. The rapid development and deep penetration of the roots of young plants aids in withstanding the critical summer drought period, while the mature root system appears superior in extent and depth to that of the annuals which are its principal competitors over much of its range.

A need for caution in generalizing on the supposedly shallow penetration of the roots of all annuals in the area is indicated by the studies of Daubenmire (1942) and Hulbert (1955) on *Bromus tectorum.* Root depths of 40-44 inches were found in several soil types in the Palouse region by both authors. Hulbert found that the fine roots of *B. tectorum* are readily broken in excavation, especially by the ice pick technique. He concluded that the difference between his results and those of other workers who have reported much shallower depths for the roots of this species is due more to differences in excavation technique than to environmental influences.

A comparison of the root system of *Hypericum* with that of the principal native perennial grass of the study area, *Agropyron spicatum* (Pursh.) Scribn. & Smith, indicated an apparent advantage for the grass. On the sites studied the root system of *Agropyron* plants was found to be more extensive, although no deeper than that of *Hypericum* plants of comparable development. This apparent superiority of the *Agropyron spicatum* root system may well be a major factor in the competition of this species with *Hypericum.* According to Weaver (1919) the root system of the other principal perennial grasses of the region, *Festuca idahoensis* Elmer. and *Poa secunda* Presl., are inferior in depth, although not in extent of fine branching to that of *Agropyron spicatum.*

Phenology

Throughout the course of the study, notes were made on the seasonal growth development of *Hypericum* and a few of the principal associated species on a number of study sites. More detailed and regular observations were made at 3 representative sites during the period 1951 to 1953 inclusive. These 3 sites included one at a low elevation in the Clearwater drainage, one at a slightly higher elevation in the Salmon River

TABLE IV. Phenology of *Hypericum perforatum* on 3 sites in northern Idaho, 1951-1953

Drainage	Elevation Feet	Start of Upright Shoots	Early Bloom	Late Bloom	Early Fruit	Ripe Seed
Clearwater.....	1200	April-1st week	June-1st week	July-2nd week	July-4th week	Sept.-2nd week
Salmon.....	1800	April-2nd week	June-2nd week	July-2-3rd week	July-4th week	Sept.-2nd week
Palouse (Moscow)..	3500	April-4th week	June-3rd week	July-4th week	August-1st week	Sept.-2-3rd week

Valley and one in high grasslands north of Moscow. A summary of the data obtained for *Hypericum* on these sites is presented in Table IV.

While the calendar dates for specific stages of growth naturally varied considerably from year to year, the pattern indicated in Table IV appeared to hold throughout the study region. First growth in spring started at about the same time as *Balsamorhiza sagittata* (Pursh) Nutt. and a week or more later than the perennial grasses *Agropyron spicatum, Poa secunda* and *Festuca idahoensis.*

The period of most rapid growth came in late April, May and the first week or two of June, a period during which favorable moisture and temperature conditions normally coincide in the study region. Differences among sites in the dates of specific growth stages tended to decrease as the season progressed, so that the mature seed stage was reached at closely similar dates on all sites. Flowering began in June and continued into July. No plants were observed to flower in their first year, but flowering was the rule in 2-year-old plants.

Hypericum remained green longer than most of the associated vegetation, including native perennials, and ranked with *Agropyron spicatum* in this respect. Shedding of *Hypericum* leaves began fairly early, however, near the end of the flowering period. By mid-August of most years the majority of plants were leafless or nearly so and the stems dry. The bulk of the seed was ripe by mid-September, and seed dissemination occurred through October and November.

The development of fresh leaf growth in the fall occurred commonly, but not in all years, or on all sites. Actually, *Hypericum* produced new fall basal growth at most sites in 4 years out of 7-year observation period (1950 through 1956). The pattern of both spring and fall growth indicated that both *A. spicatum* and *Poa secunda* began growth at lower temperatures than did *Hypericum*

The fall basal growth of *Hypericum* remained essentially procumbent, and varied from 1 to 5 inches or more in length. In spring, the basal growth showed activity 1 to 2 weeks before upright shoots began to develop. In 1952 the seasonal deficiency of soil moisture continued longer than usual, until the latter half of November. At this time temperatures were evidently too low for new growth to begin. Basal procumbent growth developed in the following March, prior to the beginning of erect shoots.

Some winter damage to the green fall growth of *Hypericum* was noted, especially on sites with erratic snow cover. The maximum damage observed was in the winter of 1950-51, before detailed studies of the plant were begun. In the early spring of 1951 it was noted that the greater part of the fall basal growth had been killed back on the majority of the plants in many localities. No plants appeared to be killed, but growth development during 1951 was apparently retarded. Native species such as *Agropyron spicatum* and *Poa secunda,* also the introduced annual *Bromus* spp., showed little or no winter damage on these same sites.

SUMMARY

Hypericum perforatum, an introduced perennial forb, has become a major weed on ranges of the Pacific Northwest and California. In Idaho, it is confined largely to the northern part of the state, and has become most abundant on depleted areas of former perennial grassland now occupied by annual grasses and forbs, particularly *Bromus* spp.

Studies were made of several features of the autecology of the species, including seed production and germination, seedling behavior, vegetative propagation, root development and phenology. The studies were conducted mainly during the period 1951-1954 as part of a larger project on the ecology and control of *Hypericum.*

Seed production during a 2-year study averaged 69 seeds per capsule, and 23,350 seeds per plant. Germination in the laboratory at temperatures of 70 to 78° Fahrenheit averaged 65 percent for a large number of samples. Seed stored indoors for 15 years gave 50 percent germination, while seed buried at depths of 1 and 3 inches retained similar viability after 3 years in the soil.

Hypericum seedlings were found only spottily in the field and seedling mortality approached 100 percent in most cases. Germination occurred principally in May and the normal seasonal drought period of late July and August proved to

be the critical period for seedling survival. The distribution pattern of the plant suggests occasional large scale establishment of seedlings under particularly favorable conditions. Vegetative propagation by root offshoots accounts for much of the local spread.

The root system of *Hypericum* seedlings commonly attains a depth of about 1 foot during its first growing season. The mature plant possesses an extensive root system which extends 4 to 5 feet in depth and about 3 feet laterally. Considerable absorption of soil moisture from depths of 30 inches or more appears to occur.

The phenology of *Hypericum* indicates a high degree of suitability to the habitat of the study area. In Idaho, spring growth begins in April, and proceeds rapidly during May and early June, when both moisture and temperature conditions are favorable. Flowering occurs in June and continues into July. Seed begins to form late in July, ripens by mid-September and is disseminated throughout October and November. Most plants are largely dried out by mid-August, but development of fresh fall basal growth occurred in 4 years out of 7 observed. This basal growth survives through the winter with only slight damage in most years and becomes active in spring 1 to 2 weeks before upright shoots begin to show.

References

Bellue, Margaret K. 1945. Weed seed handbook, series III. Calif. Dept. Agri. Bull. **34**: 116-123.

Cashmore, A. B. 1939. A note on the germination of St. John's Wort seed. Jour. Coun. Sci. Industr. Res. Aust. **12**: 181-182.

Clark, Nancy. 1953. The biology of St. John's wort (*Hypericum perforatum* L. var. *angustifolium* DC.) in Ovens Valley, Victoria, with particular reference to entomological control. Aust. Jour. Bot. 1(1): 95-120.

Columbia Basin Inter-Agency Committee, Noxious Weed Control Task Force. 1952. Noxious weeds in the Columbia Basin. Portland, Oregon. 12 pp. and maps (processed).

Daubenmire, Rexford F. 1942. An ecological study of the vegetation of southeastern Washington and adjacent Idaho. Ecological Monog. **12**: 53-79.

———. 1952. Forest vegetation of northern Idaho and adjacent Washington and its bearing on concepts of vegetation classification. Ecological Monog. **22**: 301-330.

Evanko, Anthony B. 1953. A test of borax control of goatweed. Northern Rocky Mountain Forest & Range Exp. Sta. Res. Note No. **134**. U.S.D.A. Forest Service.

Evans, Jerome. 1952. Personal communication.

Fosberg, M. A. 1956. Unpublished data. Dept. of Agronomy, Univ. of Idaho.

Harris, Grant A. 1951. St. Johnswort on western ranges (a review of literature and bibliography). Northern Rocky Mountain For. and Range Exp. Sta. Paper No. **26**: 18 pp. U.S.D.A. Forest Service.

Harshman, Edmund P. 1956. The changes in vegetation following biological control of *Hypericum perforatum*. MS. Thesis. Univ. of Idaho, Moscow, Idaho.

Huffaker, C. B. and J. K. Holloway. 1949. Changes in range plant population structure associated with feeding of imported enemies of Klamath weed (*Hypericum perforatum* L.). Ecology **30**: 167-175.

Hulbert, Lloyd C. 1955. Ecological studies of *Bromus tectorum* and other annual bromegrasses. Ecological Monog. **25**: 181-213.

Marsh, C. D. and A. B. Clawson. 1930. Toxic effects of St. Johnswort (*Hypericum perforatum* L.) on cattle and sheep. U.S.D.A. B.P.I. Tech. Bull. **202**: 1-24.

Morris, Melvin and Joseph Meuchel. 1956. The problem of St. Johnswort, a noxious plant in western Montana. Mont. For. & Conserv. Expt. Sta. Bul. **4**. Montana State Univ., Missoula.

Muenscher, W. C. 1951. Poisonous plants of the United States. The Macmillan Company, New York. 266 pp. illus. revised edition.

Piper, C. V. 1906. Flora of the State of Washington. Contrib. U. S. Nat. Herb. Vol. XI.

Pringle, William L. 1952. The ecology and control of St. Johnswort in Idaho. M.S. Thesis. Univ. of Idaho, Moscow, Idaho.

Salisbury, E. J. 1942. The reproductive capacity of plants. Bell and Sons. London. 244 pp.

Sampson, A. W. and K. W. Parker. 1930. St. Johnswort on range lands of Californa. Calif. Agr. Expt. Sta. Bul. **503**. Berkeley, Calif. 48 pp.

U. S. Department of Commerce. 1951-1956. Climatological data, Idaho. Vols. LIV-LIX.

Weaver, J. E. 1919. The ecological relations of roots. Carnegie Institution of Washington. Washington, D. C. 128 pp. illus.

Wilson, Frank. 1943. The entomological control of St. John's wort (*Hypericum perforatum* L.) with special reference to the insect enemies of the weed in southern France. Coun. Sci. Industr. Res. Aust. Bull. **169**. Melbourne, Aust. 87 pp.

SEASONAL VARIATIONS OF THE PHOTOSYNTHETIC EFFICIENCY OF EVERGREEN CONIFERS

PHILIPPE F. BOURDEAU
School of Forestry, Yale University

Studies of total dry matter production, such as those of Ovington (1956, 1957), have indicated that, in the temperate zone, evergreen conifers are in general more efficient than deciduous hardwoods. This superiority is attributed to the evergreen characteristic, which should make CO_2 assimilation possible throughout the year, whenever environmental conditions are favorable. Indeed, net photosynthesis has been found to occur during winter in coniferous species, even at low temperatures (Freeland 1944, Parker 1953). It is, however, questionable, whether the "winter" rates are comparable in magnitude to the "summer" rates, even when measured at the same temperature and light intensity. It was postulated in this study that photosynthetic efficiency, or capacity, varies throughout the year as do the degree of cold hardiness, the nature and concentration of food reserves, and many other physiological characteristics. In one experiment, the photosynthetic efficiency of Norway spruce (*Picea excelsa* Link) and blue spruce (*Picea pungens* Engelm.) trees, growing outdoors, was followed for a period of one year. In another, similar measurements were made, from November to May, on eastern hemlock (*Tsuga canadensis* (L.) Carr) and Scotch pine (*Pinus sylvestris* L.) plants kept outdoors and indoors, under short and long days. Finally, the changes in photosynthetic efficiency induced by a sudden alteration of the temperature regime were followed in Scotch pine plants.

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EXPERIMENT 1

Materials and Method

Two Norway spruces and two blue spruces, nine years old and about five feet high, were selected from a plantation at Valhalla, New York. Two current-growth twigs were cut from each tree at thirteen different dates extending over a one-year period, the first collection being made shortly after bud opening in May. Any new growth that was present at the last date of collection was removed from the sample twigs, which were then one year old. The excised twigs, their bases inserted in a small container of water, were immediately brought into the laboratory and placed in a cylindrical Lucite chamber for determinations of photosynthetic efficiency and of respiration.

The criterion chosen to estimate photosynthetic efficiency was the rate of CO_2 uptake of the twigs under uniform conditions of light and temperature, in this instance at $25 \pm 0.5°$ C. and 2,000 foot candles (about 50,000 ergs/cm^2/sec. of visible light with the source used). Respiration was measured by the CO_2 output in darkness.

Temperature was maintained constant by controlling the circulation of cold water in a jacket enveloping the chamber. The rate of CO_2 exchange by the plant tissue was estimated by measuring the rate of change in CO_2 concentration in a closed system consisting of the chamber, the sampling tube of a Liston-Becker infrared gas analyzer, a pump, and plastic tubing. The CO_2 content of the system was always maintained within $\pm$ 10% of 300 p.p.m. The measurements were first made on the entire twigs, then on the needles and stems separately.

Water content was determined by oven-drying, chlorophyll by spectrophotometry (MacKinney 1941), and nitrogen by the micro-Kjeldahl method (A.O.A.C. 1955).

Results

The average rates of net photosynthesis and respiration of the entire shoots and the average chlorophyll content of the needles are presented in Figure 1. In May, net photosynthesis was negative and respiration rates were high. At that time, the succulent twigs were elongating and the light color of the needles indicated a low chlorophyll content. Photosynthesis began to exceed respiration in early June and maximum photosynthetic rates were attained at the end of the growing season, in October and November. On December 18th, after the first heavy frosts had occurred ($-$ 10° C. on the 12th and $-$ 9° C. on the 16th), net photosynthesis was reduced to values around zero in all twigs even though the measurements were made at 25° C. and 2,000 foot candles. This condition persisted until March when rates began to increase again and, by mid-April, had reached a level comparable to the maxima observed the preceding fall.

Respiratory rates were high in the elongating twigs, decreased first sharply, and then levelled

off at the same time as net photosynthesis reached its first peak. This coincided with the end of the first flush of growth. Concomitantly, the nitrogen content of the twigs decreased from 4.75% of the dry weight in May to 1.87% in November. Respiration was at its minimum in January and February, after which time it increased again.

The chlorophyll content, very low initially, increased steadily to a maximum in October, declined slightly in December, and increased again in the spring.

The measurements made separately on stems and needles indicated that, per gram fresh weight, the stems respired several times as rapidly as the needles during the period of elongation. The stems carried on photosynthesis during the first spring and the early summer, as might be expected from their green appearance, but not enough to reach the compensation point. For example, on June 5, the average CO_2 output of the young blue spruce stems was 64 micrograms/minute/gram fresh tissue in the light, and 92 micrograms in darkness.

These results indicate, first, that it took several weeks after bud opening before the new growth contributed positively to dry matter production. Secondly, the photosynthetic apparatus lost most of its efficiency during the winter months. This decline was accompanied by a reduction in respiratory rate and by a slight decrease in the chlorophyll content of the needles. Finally, as shown in Figure 1, the average values for the Norway and for the blue spruces were very similar throughout the testing period.

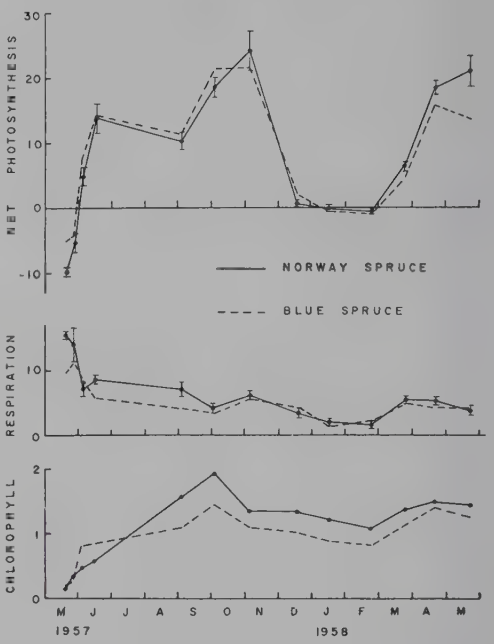


FIG. 1. Time-course of photosynthetic efficiency, respiration, and chlorophyll content in current-year (1957) twigs of Norway and blue spruces. Net photosynthesis and respiration in micrograms CO_2 exchange/minute/gram fresh twig at 25°C., at 2,000 foot candles and in darkness, respectively. Chlorophyll in milligrams/gram fresh needles. Vertical bars indicate size of standard errors of average rates in Norway spruce. Those for blue spruce are of the same magnitude.

EXPERIMENT 2

Materials and Methods

Five potted hemlocks, eight years old and about three feet high, were assigned in October to each of four treatments: outdoors, natural photoperiod; outdoors, 16-hour photoperiod; indoors, natural photoperiod; indoors, 16-hour photoperiod. The "indoor" plants were kept in a greenhouse where the temperature was not allowed to fall below 15° C. The supplementary light in the long-day treatments was provided by incandescent bulbs giving about 30 foot candles at plant level.

Measurements of CO_2 exchange under standard conditions (25° C., 3,000 foot candles and in darkness) and of chlorophyll content were made on excised current-growth twigs, following the procedure outlined for Experiment 1. Wherever present, the new growth at the end of the twigs was removed before making the determinations. Data were obtained at six dates from November to May. In addition, similar measurements were made from February to April on potted Scotch pines of the Riga strain, four years old and 2½ to 3 feet high, subjected to the same treatments.

Results

Within each temperature regime (indoors and outdoors), photoperiod had no significant effect. Thus, the points plotted in Figure 2 represent combined averages of both subtreatments, i.e. of 20 determinations in most cases (16 for the February-to-March values of the "indoor" plants because of accidental loss of two plants).

The photosynthetic efficiency of the plants left outdoors declined considerably during the winter. In January and February, net photosynthesis was negative in every tested twig. By April, the rates had increased to the level of the preceding autumn. The plants kept in the greenhouse showed a slight but statistically significant decrease in rate in January and February, as compared with November and March. At the beginning and at the end of the period, the rates of the "indoor" and "outdoor" plants were not significantly different.

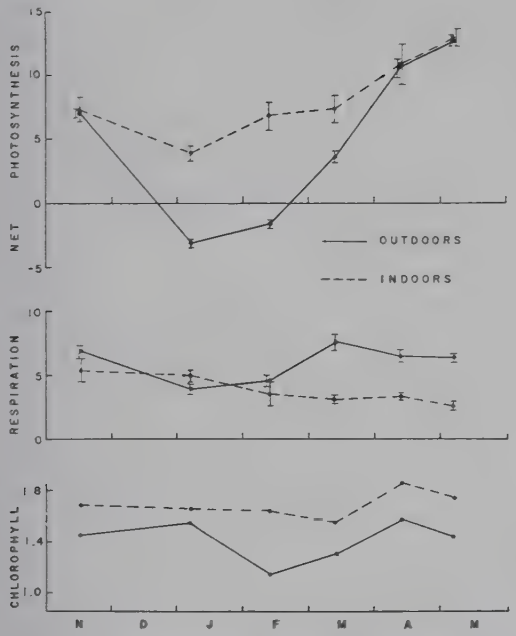


FIG. 2. Photosynthetic efficiency, respiration, and chlorophyll content in eastern hemlock kept over winter indoors and outdoors. Net photosynthesis and respiration in micrograms CO_2 exchange/minute/gram fresh twig at 25°C., at 3,000 footcandles and in darkness, respectively. Chlorophyll in milligrams/gram fresh needles. Standard errors of average rates indicated by length of vertical bars.

Respiratory rates were similar for all plants from November to February and the slight decline between November and January was not statistically significant. In the spring, on the other hand, respiration of the "outdoor" plants was significantly higher than that of the "indoor" plants. This may have been due to a higher content of soluble carbohydrates in the "outdoor" plants, since in general low temperatures favor the transformation of starch to sugar. Moreover, at that time, the greenhouse plants had started to produce new shoots which probably obtained food from the previous year's growth.

The water content of the needles was not markedly affected by treatment (112% of dry weight outdoors, and 128% indoors, on the average), thus, expressing the data per unit weight of dry needles would not alter the pattern of variation. The chlorophyll content of the "indoor" plants was higher at all times but the difference was greatest in February when the "outdoor" plants reached their minimum content of chlorophyll. The difference in coloration was in fact quite obvious. However, the chloroplasts of the "outdoor" needles appeared to be quite normal.

In general the hemlock trees left outside showed the same pattern of variation in photosynthetic efficiency as the spruces did at the same time. The greenhouse plants exhibited only a slight but significant winter minimum which could not be related to photoperiod, nor, obviously, to low temperatures.

The Scotch pines behaved very much like the hemlocks. Photoperiod had no apparent effect. In February the "outdoor" plants had a net photosynthetic rate of 0.2 micrograms CO_2/minute/gram fresh needles, as compared to 26.3 micrograms for the "indoor" plants. In early April, however, the respective values were 8.1 and 21.8 micrograms. Respiration was also higher in the outdoor plants at both dates.

Experiment 3

To determine how rapidly the pines would change from the "outdoor" to the "indoor" condition, six plants were brought into the greenhouse during March. Within five days, the average net photosynthetic rate of excised twigs increased from 3.5 to 14.5 micrograms CO_2/minute/gram fresh needles. There was a concomitant greening of the needles already apparent after the first two days. This was particularly noticeable because the Riga stain is characterized by a marked yellowing of its needles during winter.

This test was repeated in a modified manner to follow more closely the increase in photosynthetic efficiency. The CO_2 exchange of the attached terminal shoot of the pines was measured continuously by using an open system. Room air was pumped at 0.2 liter/minute through the chamber and its CO_2 content before and after passing over the shoot was recorded alternatively. Three plant chambers could be handled simultaneously by using a switching device consisting of an interval timer, a stepping switch and six solenoid valves. In this manner each plant was under measurement for ten out of every thirty minutes.

The terminal shoots of all of the plants used in these tests had negative photosynthetic rates when brought indoors. Three out of nine reached positive rates of net photosynthesis in less than 24 hours, and the balance after less than 48 hours. Actually, total photosynthesis started to increase in some cases only after two or three hours.

During the first 24 hours, the average cholophyll content increased significantly from 0.85 to 0.95 mg./g. fresh needles.

Discussion

The photosynthetic efficiency of the four species of evergreen conifers used in this study varied considerably with the season. In plants left out-

doors, net photosynthesis was reduced to zero or to negative values during the winter and this decrease in efficiency was accompanied by a decrease in chlorophyll content. Scotch pine plants could be made to change to relatively high levels of photosynthetic efficiency by bringing them indoors, at least by the end of the winter. This change occurred in one or two days and chlorophyll content increased simultaneously. Net photosynthesis decreased only slightly in the hemlocks kept in the greenhouse during winter.

It seems that low minimum temperatures induced the reduction in photosynthetic efficiency in early winter. As indicated by the behavior of the greenhouse hemlocks and of the pines brought indoors, a temperature regime with minima at or above 15°C. was adequate to either maintain or restore relatively high levels of photosynthetic efficiency. Photoperiod had no apparent effect on photosynthetic rates, either indoors or outdoors. Leaf hydration was not significantly affected by the various treatments. The reduction in photosynthetic capacity may be related to the slight decline in chlorophyll content, and to changes in protoplasmic viscosity and other modifications associated with winter hardening. Stomatal mechanism may also conceivably be altered. Measurements of stomatal opening by infiltration techniques and on collodion peels were inconclusive. It seems unlikely that photosynthesis was hindered by stomatal closing since respiration was not. In fact respiration was higher in the "outdoor" plants and their respiration rates were generally higher, in absolute values, than the photosynthetic rates.

Of interest is the slight but significant winter reduction in photosynthetic efficiency of the plants kept in the greenhouse. Since photoperiod had no effect, the only changes in environment under these conditions would be a lower average light intensity and a slightly different light quality in winter. Possibly, the variation corresponds to an endogenous rhythm.

There are few reports in the literature on the fluctuations of photosynthetic rates, when measured under uniform conditions of light and temperature. Clark (1956) followed the CO_2 uptake of needles of various ages, in white spruce and balsam fir, from May to October, in Canada. During that period, little variation occurred within each age-class, except for the new needles. Net photosynthesis did not become positive before mid-June, slightly later than the Norway and blue spruces used in the present study, as might be expected from the difference in latitude. Pisek and Winkler (May 1958) reported the results of an investigation very similar in certain respects to the present one. Under standard conditions (12°C. and 10,000 lux), they followed the CO_2 uptake of excised twigs of *Picea excelsa* Link and *Pinus cembra* L. and found the same pattern of variation, with minima in winter correlated with the minimum temperatures. They mentioned a Russian work (Iwanow and Orlowa, 1931) in which the same general results were obtained in Scotch pine. Pisek and Winkler also reported that, as was found here in Scotch pine, the photosynthetic efficiency of the twigs could be made to increase, during winter, by raising the temperature for a few days. MacGregor and Kramer (personal communication) have recently followed the seasonal trends in the photosynthetic capacity of loblolly pine and eastern white pine and also observed a marked winter minimum.

Further experiments are planned to investigate in greater detail the change of the photosynthetic apparatus from the "winter" to the "summer" condition, as well as the slight reduction in efficiency, in winter, of the plants kept indoors, under long or short days.

The results obtained by Pisek and Winkler and in the present study indicate that it is erroneous to assume that evergreen conifers are able to produce dry matter at high rates, at any time of the year, whenever temperature and light intensity are favorable.

Summary

CO_2 exchange under uniform conditions of light and temperature was measured in young shoots of Norway and blue spruces, for a period of one year, starting shortly after bud opening. Net photosynthesis became positive in June and reached its maximum at the end of the growing season. It decreased to negligible levels in winter and increased again during the following spring. A decrease in chlorophyll content accompanied this winter decrease in photosynthetic efficiency. Respiration varied also through the year, with the lowest rates occurring in winter.

The same pattern was observed in eastern hemlocks and Scotch pines kept outdoors under either short or long days, while there was only a slight winter depression in photosynthetic efficiency if the plants were left in a heated greenhouse. When brought indoors, Scotch pines changed from negative to positive net photosynthesis in less than 2 days.

The seasonal fluctuations in photosynthetic capacity, with a marked winter minimum, indicate that the evergreen habit does not necessarily enable conifers to carry on appreciable photosynthe-

sis during the cold season, whenever the environmental conditions are favorable.

References

Association of Official Agricultural Chemists. 1955. Official methods of analysis of the Association of Official Agricultural Chemists. 8th Ed. Washington, D. C., 1008 pp.

Clark, J. 1956. Photosynthesis of white spruce and balsam fir. Canada Dept. Agric. Science Service. Forest Biol. Div. Bi-monthly Progress Report 12(5): 1-2.

Freeland, R. O. 1944. Apparent photosynthesis in some conifers during the winter. Pl. Phys. **19:** 179-185.

Iwanow, L. A., and I. M. Orlowa. 1931. Zur Frage über die Winter-assimilation von Kohlensäure unserer Nadelhölzer. Z. russ. bot. Ges. **16:** 139. [In Russian. Original not seen. Quoted by Pisek and Winkler. 1958.]

MacKinney, G. 1941. Absorption of light by chlorophyll solutions. J. Biol. Chem. **140:** 315-322.

Ovington, J. D. 1956. The form, weights and productivity of tree species grown in close stands. New Phytol. **55:** 289-304.

———. 1957. Dry-matter production by *Pinus sylvestris* L. Ann. Bot. N. S. **21:** 287-314.

Parker, J. 1953. Photosynthesis of *Picea excelsa* in winter. Ecology **34:** 605-609.

Pisek, A., and E. Winkler. 1958. Assimilationsvermögen und Respiration der Fichte (*Picea excelsa* Link) in verschiedener Höhenlage und der Zirbe (*Pinus cembra* L.) an der alpinen Waldgrenze. Planta **51:** 518-543.

THE ECOLOGY OF JAMAICAN CORAL REEFS
I. SPECIES COMPOSITION AND ZONATION[1]

Thomas F. Goreau

Physiology Department, University College of the West Indies and The New York Zoological Society

Introduction

This paper, the first of a series, is intended to serve as a descriptive introduction of the corals of Jamaica, and to give the results of a preliminary survey of zonation and growth forms of scleractinian populations on Jamaican reefs.

The investigation of Jamaican corals began with Sir Hans Sloane (1707) and Dr. Patrick Browne (1756) who figured a number of "zoophyta" in their respective natural histories of the island. However, the systematic study of Jamaican corals did not begin until Duerden (1902, 1904) published his classic monographs on the structure, development and biology of West Indian madreporaria, most of which he collected near Kingston and Port Royal. Unfortunately, Duerden gave little information on localities and none on ecological relationships, and made no attempt to describe the reef habitat as a whole. The madreporarian collection at the Institute of Jamaica (Fontaine 1954) includes some of Duerden's specimens, but it is still incomplete at the time of writing.

During the past three years, the author has had the opportunity to carry out a series of field and laboratory investigations on Jamaican reef building corals. A complete collection has been assembled, which will eventually be deposited at the United States National Museum.

[1] A part of the material in this paper was taken from a doctoral dissertation submitted by the author to Yale University.

West Indian reefs in general, and Jamaican reefs in particular, are on the whole very much smaller than their Indo-Pacific counterparts. Nevertheless, Colman's assertion (cf. Steers 1940 p. 306) to the effect that "Jamaican reefs are far from typical coral formations" and the further implication that most of them are not holding their own is based, as will be seen below, on incomplete evidence derived from observations carried out on a small number of reefs which happened to be located in that part of Jamaica visited by the Cambridge Expedition of 1939. Whereas the number of scleractinian species in West Indian reefs is at best less than one third that known to occur, for example, on the Great Barrier Reef or in the Marshall Islands (Wells 1954), the density of coral growth is in many localities comparable. Also, the calcareous algae which form between forty and ninety per cent of the reefs in Bikini Atoll (cf. Johnson 1954), play a very much less conspicuous role in the building up and consolidation of West Indian reefs. For a comparison of zonation and species composition of reefs in several Pacific atolls the reader is referred to the papers of Wells (1951, 1954) and Emery *et al.* (1954).

Method

The methods used in the ecological study reported in this paper were extremely simple. The reefs described were readily accessible by small boat during calm weather. Initial transects were

run by swimming across the reef with fins, mask, breathing tube, and a geological hammer with which to collect specimens. In this way, the reef could be observed to depths of about fifteen meters. Detailed transects were run with the aid of a sounding line marked off in meters, and the approximate number of corals of different species in the range of vision at various stations was noted. Underwater photographs were taken in representative areas and sketches and field measurements were recorded on an underwater drawing board made of roughened white plexiglass. The great majority of the field observations were carried out by mask diving, but some work in deeper parts of certain localities had to be done with the aid of a self contained diving unit of the oxygen recirculator type. In Barbados, most of the reef surveys in deeper waters were made with an Aqualung.

Grateful acknowledgments are due to the following: Professor D. M. Steven of the Zoology Department of the University College of the West Indies, for making available a boat and other facilities of the University's Marine Station in Port Royal; Mr. Lachlan Macneil, Ocho Rios, for his personal interest and assistance in surveying the Ocho Rios reefs; Dr. V. A. Zans and Professor Normal Newell for stimulating discussions of certain points of geological interest; Captain E. G. Irving, O.B.E., R.N. for kindly making it possible to carry out aerial photosurveys of some Jamaican north coast reefs from the helicopter of H. M. Admiralty Survey Ship *Vidal;* Dr. Arthur Fontaine of the Institute of Jamaica who assisted with the initial identification of some of the coral species; Dr. John Lewis, Director of the Bellairs McGill Research Institute in Barbados for his hospitality and help during a short trip to the eastern Caribbean that was supported by an institutional grant from funds provided by the Carnegie Foundation. Much of the work reported in this paper was supported by a grant from the New York Zoological Society. The geological map shown in Figure 1 is reproduced with the kind permission of Dr. V. A. Zans, Director of the Geological Survey of Jamaica.

General Description of Jamaica

Jamaica is a large tropical island about 125 miles long and 50 miles wide, 18° 30′ degrees north of the equator. It is located in the center of the Carribean area just south of Cuba and west of Hispaniola.

Geologically, the island is a low dome built up on a core of upper Cretaceous rocks which are unconformably overlain by a sedimentary mantle ranging in age from Eocene to Recent (V. A. Zans, private communication). More than two thirds of the surface is covered by limestones of different kinds. The coastal formations on the north shore are mainly hermatypic limestones of Miocene to Pleistocene age, whereas the south shore is built up of older limestones and extensive Recent alluvial deposits that fan out from the central highlands (see Figure 1).

Along the greater part of the coastline, the offshore shelf is relatively narrow so that the 20-fathom contour lies mostly less than 500 meters from land except in the region between Kingston and Black River where there is a large offshore shelf 15 miles wide by about 80 miles long.

Jamaica lies in the belt of the northeasterly tradewinds, but the island is large and high enough so that a semi-continental climate exists in the interior. Local factors combine to alter considerably the pattern of the prevailing surface winds in different parts of the island. According to Pilsbury (1951) 90% of the surface winds above 15 miles per hour at Palisadoes Airport on the south coast near Kingston blow from a southeasterly direction. On the other hand, on the northwest coast at Montego Bay Airport, surface winds above 15 miles per hour blow from a northeasterly direction about 75% of the time.

The surface temperature of coastal waters varies between 24°C in January and 27.5°C in July. Higher temperatures are often encountered in harbours and lagoons where circulation is restricted. The tides are irregular, tending to "double up" so that they occur only once a day. They vary in height between 20 and 36 centimeters. There is a well defined westward current on both coasts which becomes more pronounced during the trade wind season between April and December.

The geographical distribution of reef tracts on the coast of Jamaica and their relation to the underlying geology is shown in the map in Figure 1. On the north coast, fringing reefs extend, with some gaps, from Morant Point in the east to Negril in the west. On the south coast however, large reefs are restricted to the eastern part of the coastal shelf near Port Royal and Old Harbour. Elsewhere on this coast reefs tend to be small, patchy and often dead.

The Jamaican Scleractinian Fauna

Of the 41 scleractinian species so far collected in Jamaica, 40 have been found by the writer and 14 are new records. Only one, *Solenastrea bournoni,* which was listed by Duerden (1902) as occurring in Kingston Harbour, has not yet been

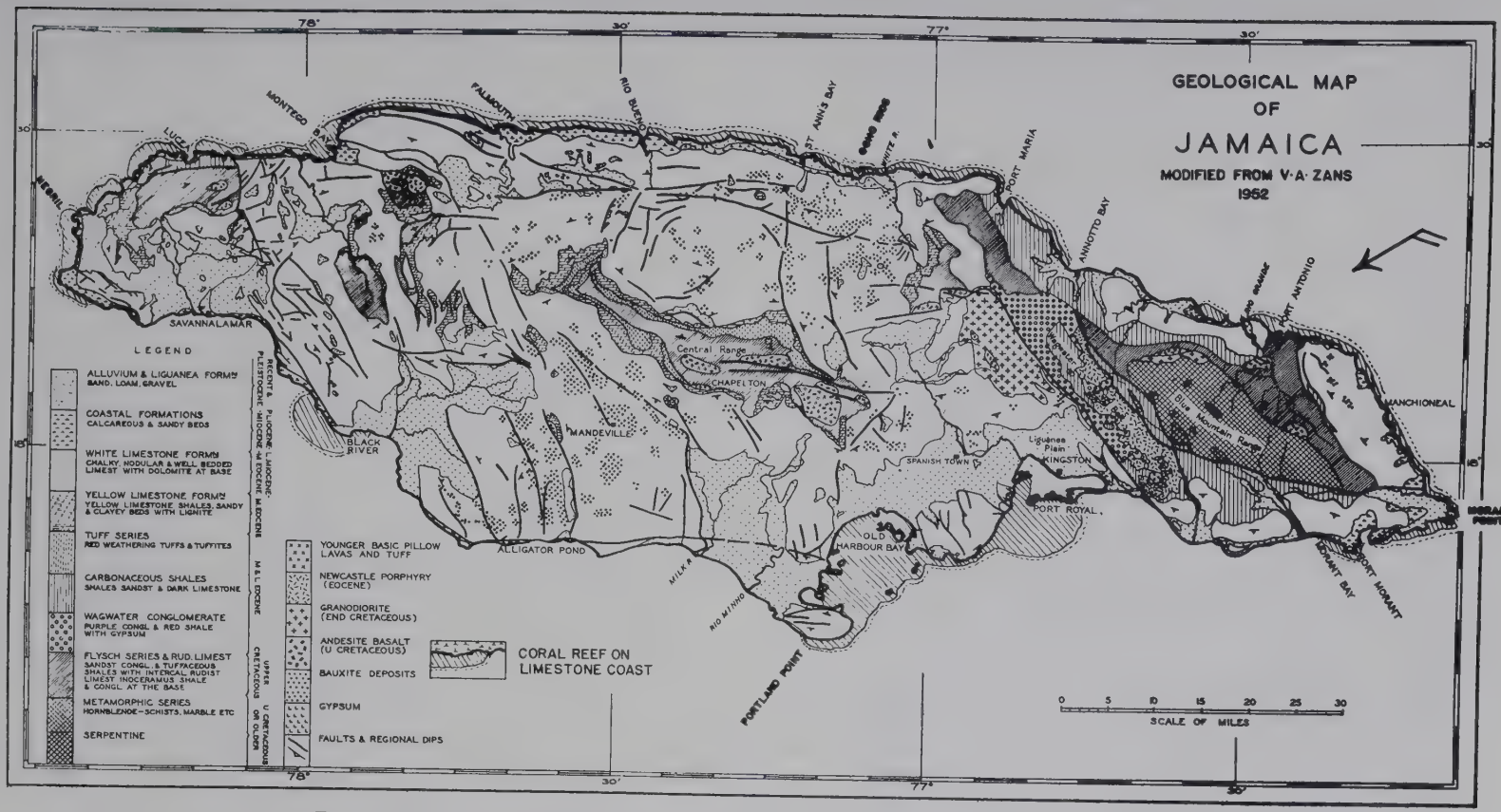


FIG. 1. Geological map of Jamaica showing the dome structure of the island with successively younger sedimentary formations at the periphery. The cross hatched parts of the seacoast represent areas in which large coral reefs are found. The map is by courtesy of Dr. V. A. Zans and the Jamaica Government Geological Survey.

TABLE I. List of Jamaican Shallow Water Scleractinia*†

Class ANTHOZOA Ehrenberg
Subclass HEXACORALLIA Haeckel
Order SCLERACTINIA Bourne
Suborder ASTROCOENIINA Vaughan and Wells
Family ASTROCOENIIDAE Koby
Stephanocoenia michelinii (Milne Edwards and Haime) D,G
Family ACROPORIDAE Verrill
Acropora palmata (Lamarck) D,G
Acropora cervicornis (Lamarck) D,G
Acropora prolifera (Lamarck) D,G
Family POCILLOPORIDAE Gray
Madracis decactis (Lyman) G
Madracis asperula (Milne Edwards and Haime) G
Suborder FUNGIINA Duncan
Superfamily AGARICIICAE Gray
Family AGARICIIDAE Gray
Agaricia agaricites (Linnaeus) D,G
Agaricia fragilis (Dana) D,G
Agaricia nobilis (Verrill) G
Family SIDERASTREIDAE Vaughan and Wells
Siderastrea siderea (Ellis and Solander) D,G
Siderastrea radians (Pallas) D,G
Superfamily PORITICAE Gray
Family PORITIDAE Gray
Porites porites (Pallas) D,G
Porites astreoides (Lamarck) D,G
Porites furcata (Lamarck) D,G
Porites divaricata (Lesueur) D,G
Suborder FAVIINA Vaughan and Wells
Superfamily FAVIICAE Gregory
Family FAVIIDAE Gregory
Subfamily FAVIINAE Gregory
Favia fragum (Esper) D,G
Diploria strigosa (Dana) D,G
Diploria clivosa (Ellis and Solander) G
Diploria labyrinthiformis (Linnaeus) D,G
Colpophyllia natans (Muller) D,G
Colpophyllia amaranthus (Muller) G
Manicina areolata (Linnaeus) D,G
Subfamily MONTASTREINAE Vaughan and Wells
Cladocora arbuscula (Lesueur) D,G
Montastrea annularis (Ellis and Solander) D,G
Montastrea cavernosa (Linnaeus) D,G
Solenastrea hyades (Dana) D
Family RHIZANGIIDAE d'Orbigny
Astrangia solitaria (Lesueur) D,G
Phyllangia americana (Milne Edwards and Haime) D,G
Family OCULINIDAE Gray
Subfamily OCULININAE
Oculina diffusa (Lamarck) D,G
Oculina valenciennesi (Milne Edwards and Haime) D,G
Family MEANDRINIDAE Gray
Subfamily MEANDRININAE Gray
Meandrina meandrites (Linnaeus) D,G
Meandrina braziliensis (Milne Edwards and Haime) G
Subfamily DICHOCOENINAE Vaughan and Wells
Dichocoenia stokesii (Milne Edwards and Haime) D,G
Dendrogyra cylindrus (Ehrenberg) G
Family MUSSIDAE Ortmann
Mussa angulosa (Pallas) G
Isophyllia multiflora (Verrill) G
Isophyllia sinuosa (Milne Edwards and Haime) D,G
Isophyllastrea rigida (Dana) G
Mycetophyllia lamarckana (Milne Edwards and Haime) G
Suborder CARYOPHYLLIINA Vaughan and Wells
Superfamily CARYOPHYLLIICAE Gray
Family CARYOPHYLLIIDAE Gray
Subfamily EUSMILIINAE Milne Edwards and Haime
Eusmilia fastigiata (Pallas) G
Suborder DENDROPHYLLIINA Vaughan and Wells
Family DENDROPHYLLIIDAE Gray
Tubastrea tenuilamellosa (Milne Edwards and Haime) G

* Classification is according to Vaughan and Wells (1943) and Wells (1956).
† The symbols D and G in superscript following the species names indicate whether species was recorded by Duerden (1902), by Goreau, or by both.

recorded by the author. Of all the shallow water species listed in Table I, only 5, belonging to the families *Rhizangiidae, Oculinidae* and *Dendrophylliidae,* can be classified as ahermatypes despite the fact that they often grow in localities where hermatypes also occur.

The finding of *Meandrina braziliensis* in Jamaica is of some interest. Smith (1948) states that this coral is found in Floridian and West Indian reefs, but localities or references are not given. There is increasing evidence that this species is found in the deeper zones of the fore reef, or seaward slope. In Barbados it is common at depths below 5 meters. Last year some colonies were recovered from a submarine cable at a depth of about 40 meters just east of Turks Island. Small colonies were recently dredged by H. M. Admirality Survey Ship *Vidal* from sandy bottom at 20 meters, 12 miles south of Milk River, Jamaica. *M. braziliensis* has not been seen growing in Jamaican reefs at the time of writing, but it is interesting to note that specimens of this coral have been found by Dr. V. A. Zans on boulder ramparts of the Pedro Cays 60 miles south west of Kingston.

Some observations on the distribution of *Tubastrea tenuilamellosa* are also of interest. In contrast to all other corals in this area which are predominantly green, yellow or brown due to their zooxanthellae, the coenosarc of *Tubastrae* is colored a bright red and zooxanthellae are absent. The clump-like colonies, which do not exceed 15 centimeters across, are sometimes found in restricted localities on very exposed coasts where they grow at shallow depths on wave swept rocks, usually together with some reef building corals. In both appearance and ecological requirements, *Tubastrea* bears an extraordinary resemblance to the Mediterranean dendrophylliid *Astroides calycularis.* No precise information is as yet available on the extent of distribution of this coral in West Indian waters as it has been previously reported only from Curacao (J. W. Wells, J. S. Zanevelt, private communication).

FIG. 2. Airphoto of the fringing barrier reef located north-east of Ocho Rios, Jamaica, and described in the text. The large cleft or canyon running diagonally through the center of the reef is an unique feature of unknown origin that is not seen in other Jamaican reefs. It appears to be unrelated to rivers or other physiographic features. The rectangle on the right hand side of the figure represents the area covered by Figure 3, and the smaller cross hatched rectangle is the region shown in Figure 5. Airphoto courtesy of the Jamaica Government Survey.

ZONAL ANALYSIS OF A LARGE REEF NEAR OCHO RIOS, JAMAICA

All larger Jamaican reefs can be divided into regions and zones on the basis of local differences in topography and species associations of corals and other bottom organisms. The reef to be described in this section is typical of the large fringing barrier reef communities found along the north coast of Jamaica; it is shown in the aerial photograph in Figure 2. This structure runs in an east-west direction at distances between 10 and 600 meters from shore and extends partly across the mouth of Ocho Rios Bay. The reef intercepts the trade wind seas tangentially so that wave action is moderate for the greater part of the year except during January, February and March when heavy seas may pound the coast during northerly gales. The transparency of the water in this area is variable, and depends largely on the degree of wind-generated turbulence which can reduce the visibility to a few meters on the fore reef and to zero in the channel or lagoon. Sediment carried into the sea by rivers also reduces the surface transparency of the water. The surface salinity may be noticeably decreased by fresh water welling into the sea from the base of the limestone cliffs which form much of the shore line of this coast. On calm days, lenses of brackish water can frequently be found on the surface several hundred meters offshore. This does not appear to have any untoward effect on coral growth except very close inshore where the cold upwelling ground water often reduces the salinity to such an extent that the water is nearly fresh to the taste.

The oxygen content of the water crossing the reef varies between 3.0 and 9.0 ml/L, depending on the light intensity, turbulence and sediment in the water. On the average sunny day, the water on the reef becomes supersaturated with oxygen as shown by the gas bubbles which collect on the coral and algae during calm weather. Our measurements show that in daytime the water crossing the reef gains between 0.6 and 2.5 ml 0_2/L whereas at night about 1 ml 0_2/L is removed by respiration.

The hydrography of these reefs is somewhat complicated by the fact that in the daytime the main driving force of the water circulation is provided by the easterly trade wind which sets up a longshore current that dies down at night with

FIG. 3 Oblique airphoto of the fringing barrier reef at Ocho Rios, Jamaica, taken with polaroid filter and extreme wide-angle lens from a helicopter at an altitude of 150 feet. This photo includes the area marked off in Figure 1, and is also diagrammed in Figure 4. The average distance between individual buttresses in the lower middle of the Figure is from 9 to 12 meters, and the development of a dendritic drainage pattern of sediment from the lower *palmata* zone into deeper water is evident. The horizontal distance through the center of this airphoto is about 200 meters.

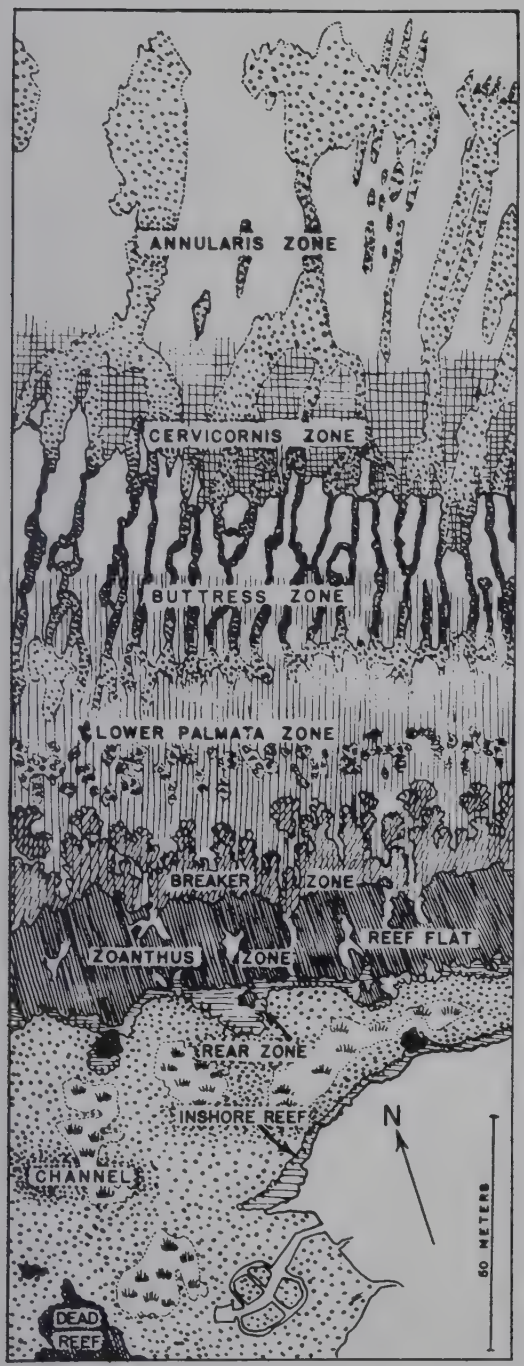
the falling of the wind. At such times water circulation on the reef becomes dependent on the ebb and flow of the tides.

The zonal structure of the reef becomes apparent by taking a profile traverse across it from shore to deep water. The different zones and regions are named according to their most conspicuous faunal or topographical characteristic. Their relationship to each other and to the reef as a whole is summarized in Table II. The appearance of this reef as a whole is seen in Figure 2 which is a vertical air photo taken from an altitude of 6,000 feet. Figure 3 is an oblique airphoto taken at an altitude of 150 feet from a helicopter. An enlarged portion of this is shown in Figure 4 while Figure 5 is an elevation view of the same area to demonstrate the cross sectional topography in detail.

Exact figures relating to the abundance or biomass of any given coral species per unit area in the different zones of the reef are not yet available. However, as a result of notes and observations during numerous transects that were made in this area, a rough approximation of the relative abundance of the different species could be obtained. This information is summarized in Table III to show the distributional pattern of corals on the reef. The number of plus signs following the species names is intended only as an indication of their relative abundance. The data are based on the relative frequency with which different scleractinian species were observed in the

TABLE II. Relationship of zones in a reef at Ocho Rios, Jamaica

Region	Zone		Average Width (meters)	Average Depth (meters)
Back-reef region	Shore zone		1- 10	0.5- 3
	Lagoon or channel		10-300	2 -15
Reef crest	Rear zone		3- 10	1 - 3
	Reef flat		20- 50	0.5- 3
	Palmata zone	Upper (breaker)	6- 10	0.5- 3
		Lower	30- 50	3 - 6
	Buttress zone		40- 60	1 -10
Seaward slope or fore-reef	*Cervicornis* zone		30- 60	7 -15
	Annularis zone		>60	15



various zones at the time these transects were made. A quantitative survey of this reef is now in progress and will be reported in a subsequent paper.

Although this study is concerned essentially only with the reef building corals, some non-reef building, or ahermatypic, species are often found underneath large colonies, in tunnels and caverns within the reef, or in certain turbid harbour localities where the oxygen content of the water is reduced. These corals may become quite numerous in certain restricted areas but their abundance in terms of aggregate biomass is nevertheless only a very small fraction of that of the hermatypic corals.

The shore zone

A mixed and frequently rich scleractinian population is often observed on rocky shores at depths up to 3 meters. The most numerous species are *Acropora palmata, Montastrea annularis, M. cavernosa, Diploria strigosa, Porites astreoides, P. porites, Siderastrea siderea* and *Manicina areolata* (on sandy bottom). Encrusting *Lithothamnion* is usually abundant on exposed wave swept rocks. Hardy species such as *Diploria clivosa, Siderastrea radians* and *Favia fragum* occur where the inshore environment is turbid and sometimes stagnant.

The channel or lagoon zone

This region is between 10 and 300 meters wide and from 2 to 15 meters deep. The bottom is sandy and there is a correspondingly sparse coral population. Gorgonians, molluscs and echinoderms occur in large numbers but the bulk of the bottom sediments of this zone are formed from foraminifera and *Halimeda* fragments, with corals contributing comparatively little. Calcareous muds often occur in depressions and stagnant inlets. Large parts of the lagoon bottom are overgrown by strips of turtle grass (*Thalassia testudinum*) in which are often found small unattached colonies of *Manicina areolata* and *Porites divaricata*. In deeper parts of the lagoon there are isolated heads of *Montastrea annularis* and hillocks formed of *Porites porites* which may reach a height of several meters.

The rear zone

This region forms the inshore limit of the reef crest. It rises abruptly from the sandy bottom of the lagoon at a depth of 2 or 3 meters and is

FIG. 4. Enlarged section of the reef in Figure 2 to show the succession of zones in greater detail. The shoreline is on the lower right and the seaward slope is at the top of the figure. The relationship of the buttress zone is clearly shown.

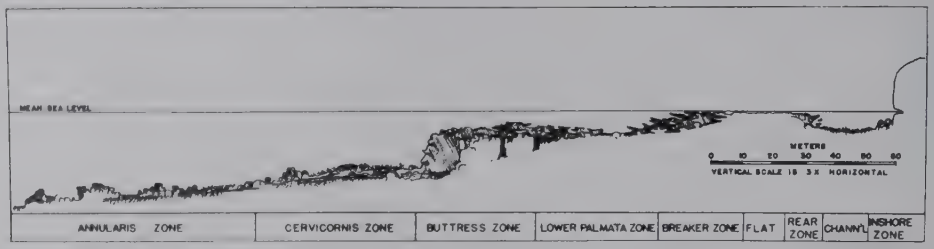


FIG. 5. Elevation view of a reef transect taken in a line coinciding approximately with a line drawn through the center of the reef area shown in Figure 2. The precipitous topography of the buttress zone is clearly indicated.

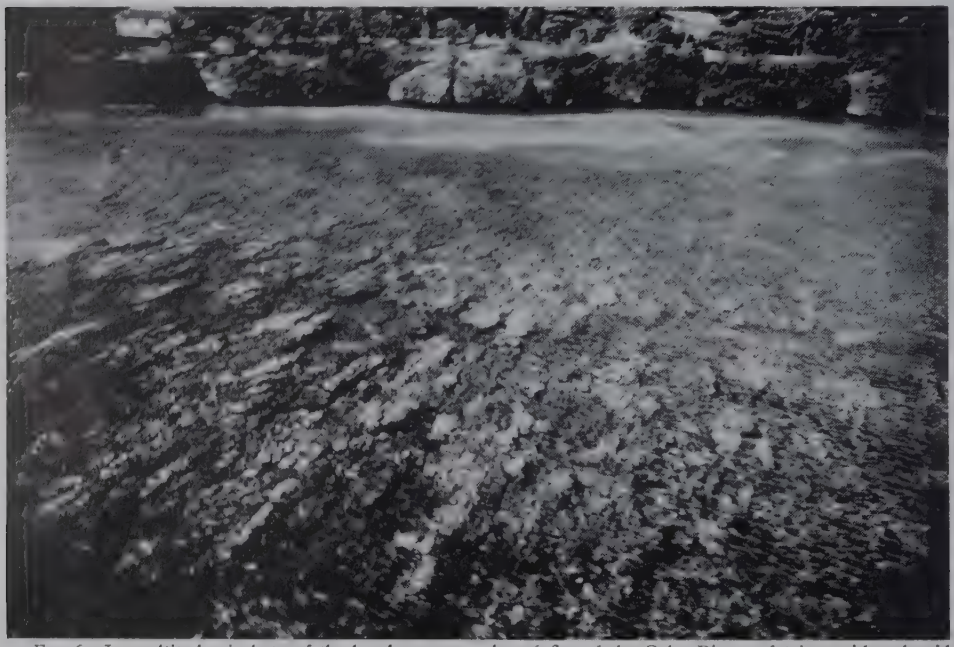


FIG. 6. Low altitude airphoto of the breaker zone and reef flat of the Ocho Rios reef taken with polaroid filter and extreme wide-angle lens from a helicopter. This shows the strongly oriented growth pattern of the *Acropora palmata* population in this region. It should be noted that this directional pattern is still preserved in the *Zoanthus* overgrown reef flat in the upper middle of this figure, showing that the killed colonies have been incorporated *in situ* into the reef flat. The horizontal distance through the center of the figure is about 60 meters.

the site of a rich and varied coral population growing almost to the surface. The massive species predominate, among them *Montastrea annularis, Diploria strigosa, Montastrea cavernosa, Siderastrea siderea* and *Porites astreoides* are the most important. Branching species such as *Acropora palmata, A. cervicornis, A. prolifera, Porites porites* and *P. furcata* are also very common though less important in regard to their biomass.

The reef flat, or Zoanthus *zone*

This is the crest of the reef which is formed almost entirely from the dead and unconsolidated colonies of *Acropora palmata* (see Figures 6 and 7). Much of this has become overgrown with a thick rubbery mat of the green colonial zoanthid *Zoanthus sociatus* which gives this region of the Ocho Rios reef its characteristic appearance. Except for a few encrusting colonies of *Diploria clivosa*, corals are scarce on the reef flat but *Millepora, Gorgonia, Lithothamnion* and *Halimeda* are fairly abundant. A rich coral fauna, resembling that of the rear zone, is found in many of the shallow channels which cross this region. In some cases, lateral coral growth blocks the channels re-

TABLE III. Distribution of Shallow water Scleractinia on the Ocho Rios Reef*

Family and Species	Tide Pools	Back Reef: Inshore Zone	Back Reef: Channel or Lagoon	Reef Crest: Rear Zone	Reef Crest: Reef Flat	Reef Crest: Palmata Zone: Upper (Breaker)	Reef Crest: Palmata Zone: Lower	Reef Crest: Buttress Zone	Seaward Slope: Cervicornis Zone	Seaward Slope: Annularis Zone
ASTROCOENIIDAE										
S. michelinii			+	++						++
ACROPORIDAE										
A. cervicornis		++	+++	+++	+	+	+++	+++	+++++++++++	++++
A. palmata		+++++	+++	++++	+++	++++++++++	++++++	+++++++	+	
A. prolifera		++	+	+++	+	+	++	++	+++	++
POCILLOPORIDAE										
M. decactis			+					++	+	
M. asperula								++	+++	++++
AGARICIIDAE										
A. agaricites	+	++	+	++	++	+++	+++	+++++++	+++	++
A. fragilis		+	+	+	+	+	+	+++	+	++
A. nobilis								+		
SIDERASTREIDAE										
S. radians	++++	+++	+++	++	++++	++	++	+		
S. siderea		+++	++++	++++	+	+	++	+++	++	+++
PORITIDAE										
P. astreoides	+	+++	++	+++	+++	+	+	++++++	++	++++
P. porites		++	+++	++	+	+	++	+++	++++++++	++++++
P. furcata		+	+	++				+++++	+++	+
P. divaricata			++	+						
FAVIIDAE										
F. fragum	++	+++	++	++	+++	+	+	+	+	
D. clivosa	++++	++++	+++	+++	+++	++	+			
D. strigosa		+++++	+++	++++	++	++++	+++	+++++	++	++++
D. labyrinthiformis		+	+	+	+	++	++	+++	+	+++++
C. amaranthus							+	+	+	++
C. natans		+	+++	+	+	+	++	+++++	++++	+++++
M. areolata		++	+++	+			+			
C. arbuscula			+							
M. annularis		++	+++	++++	+	+	+	++++++++++	+++++++	++++++++++
M. cavernosa		+++	+++	+++	+		+	+	+	++
RHIZANGIIDAE										
P. americana		+	+							
A. solitaria		+	+	+			+	+	+	+
OCULINIDAE										
O. diffusa		+	+							+
O. valenciennesi										+?
MEANDRINIDAE										
M. meandrites		+	+					+	+	++
M. braziliensis										++?
D. stokesi		++	+	++	+		+	+	+	+
D. cylindrus				+	+		+	+	+	+
MUSSIDAE										
M. angulosa				+			+	++	+	++
I. rigida		+	+	+			++	+	+	+
I. multiflora		+	+	+				+	+	+
I. sinuosa		++	++	++			+	+		
M. lamarckana		+		+			+	++	+	+
CARYOPHYLLIIDAE										
E. fastigiata		++	+	+			+	+	+	++
DENDROPHYLLIIDAE										
T. tenuilamellosa		+						+		
MILLEPORINA										
M. alcicornis		++	+	+	+++	++++	+++++	+++++	++	+
STYLASTERINA										
Stylaster sp.								+	+	+

*The number of plus signs following the species names in this table is not to be interpreted as having quantitative connotations other than that it corresponds to averages of rough species counts made on this reef during repeated traverses. Arbitrarily, 1 plus can be taken to mean rare; 2 plus is scarce; 3-4 plus is common; 5-7 plus is abundant and 8-12 plus is very abundant.

sulting in the formation of isolated pools. This zone is on the average 40 meters wide and less than half a meter deep except in the channels and pools where the depth may increase to over 2 meters.

The palmata zone

In the upper, or breaker, region of this zone, the *Zoanthus* overgrown reef flat abruptly gives way to a narrow zone which is populated almost exclusively by huge tree-like colonies of *Acropora*

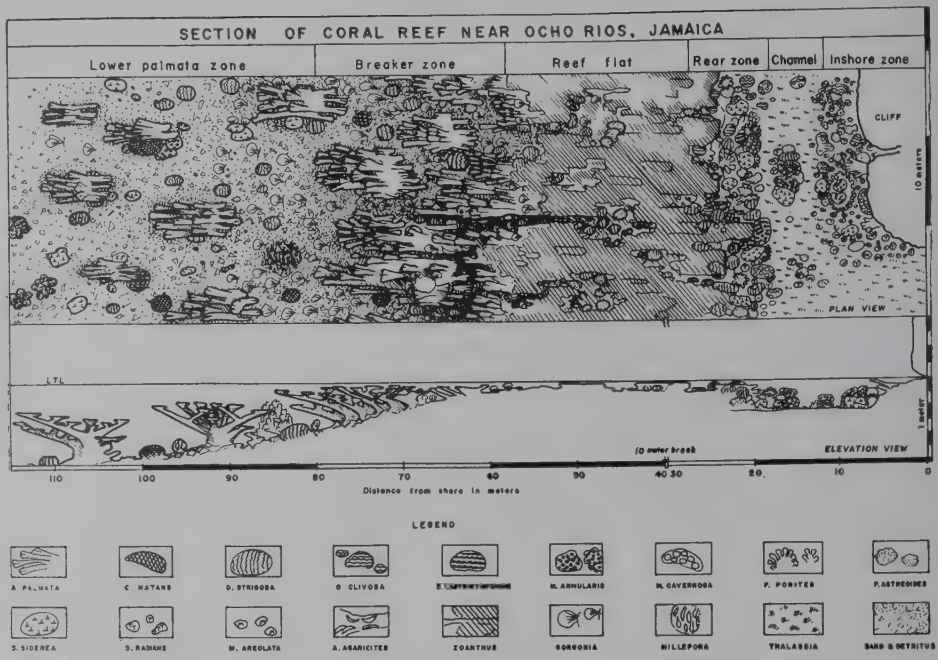


FIG. 7. Detailed plan view of the crest and back reef zones of the Ocho Rios reef to show the distribution pattern of individual coral colonies in this region. The size of individual corals is exaggerated about 4 times and the actual number of colonies is therefore reduced by a proportional amount. The shoreline is on the right hand side of the figure.

palmata that take the full force of the surf. The great serried outliers of this coral are predominantly oriented in the direction of the prevailing seas which thus give the whole zone the characteristic appearance of a great jagged comb with irregular teeth. This can be seen in Figures 6, 7 and 8. In this region, *Acropora palmata* is clearly dominant and exists as a nearly pure population except on the sides of surge channels where *Diploria strigosa, Porites astreoides, Agaricia agaricites* and other corals may be found in some numbers. *Millepora alcicornis* often forms great heads which, like *Acropora,* take the full force of the surf. *Gorgonia* and *Lithothamnion* are common on dead coral, and the bottom is in many places littered with broken, dead and overturned colonies of *Acropora palmata.*

In front of the breaker zone, the reef slopes gently downward to depths of between 5 and 6 meters over a distance of from 30 to 60 meters. This lower *palmata* region forms a kind of moat since the reef becomes shallower again in the buttress zone which is the next zone to the seaward (see Figure 4). *Acropora palmata* is still the dominant coral, growing in large isolated heads that also are strongly oriented into the prevailing seas. The density of living coral is much reduced in comparison to the breaker zone, and large areas of the bottom are covered with unconsolidated rubble on which coral growth is sparse.

The deeper parts of this zone have a more diverse coral population, consisting of *Diploria strigosa, Montastrea annularis, Acropora cervicornis, Colpophyllia natans, Porites astreoides, P. porites, P. furcata, Agaricia agaricites,* mussids, and *Millepora* scattered among some larger heads of *Acropora palmata.* Foraminifera together with *Halimeda* and other calcareous algae are abundant, forming more than 60% of the bulk of the finer sediments.

The buttress zone

Along the greater part of the reef, the lower *palmata* zone merges abruptly into a region of spectacular underwater scenery. The most remarkable features of this zone are huge spurs or buttresses of living coral which project outward into much deeper water. These are separated from each other by a series of very narrow, somewhat winding, canyons the walls of which are perpendicular or even overhanging. This can be

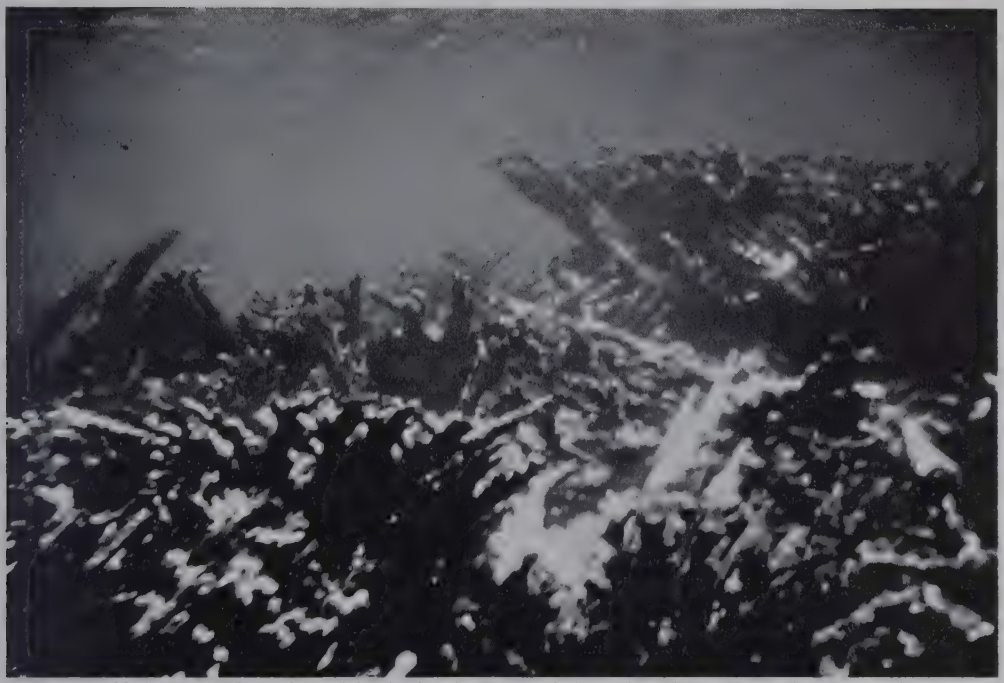


FIG. 8. Underwater view of coral in the breaker zone of the Ocho Rios reef showing the dominant population of *Acropora palmata* that is characteristic of this region. The top of the coral outlier on the right of the figure is only a half a meter below the water surface. A large still living colony which has been tilted on its side can be seen on the left, and some killed and partly broken up *A. palmata* is shown in the center. The depth here is about 3 meters and the horizontal distance through the center of the figure is about 15 meters.

seen in the underwater photograph in Figure 9. The buttresses and canyons run roughly parallel to each other in a direction that is always normal to the reef front. At the buttress crests, the depth averages only about 2 meters whereas the canyons are between 8 and 10 meters deep.

The alternation of buttress with canyon on the Ocho Rios reef is surprisingly uniform over considerable distances. Large scale aerial survey photographs show that this zone extends, with a few interruptions, along the north coast from Port Antonio in the east to Montego Bay in the west, a distance of about 130 miles. An example of the topography of this zone is given in figure 10 which shows the results of a series of cross sectional and longitudinal transects in the buttress zone of the reef opposite "Sombra," near Ocho Rios. In this region, the crest-to-crest distance between the coral spurs averages 8 meters, the width of the canyons being between one and 2 meters, but in some cases they were seen to be as wide as 10 meters or more. More recently, however, we have seen from the air considerably larger buttresses and much deeper canyons in the reef area between Oracabessa and Salt Gut some 10 miles east of Ocho Rios such as are shown in Figure 11. There appears to be considerable local variation in the degree of development of this zone although the overall characteristics described in this paper seem to apply in all those areas which we have so far explored.

The spurs of the buttresses usually terminate abruptly to form a steep promontory jutting out into deeper water, as shown in Figure 12. The canyons, on the other hand, continue outward across the fore reef as strips of sand for distances of several hundred meters. The buttress zone is by far the richest in the reef from the point of view of biomass of living coral per unit area. More than 90% of the available surface is covered by living coral, the exception being the narrow sand strips at the bottom of the canyons from which coral is usually absent.

Along the greater part of the reef, the buttresses support a large population of *Agaricia agaricites*, this being the only region where this species may become co-dominant as seen in Figure 13. The extreme hardness and toughness of this coral probably accounts to some extent for the resistance of the buttresses to storm damage. Also abundant on the spur crests are large tree-like growths of *Acropora palmata*, great multilobar

FIG. 9. Vertical underwater view into a canyon between 2 buttresses in the Ocho Rios reef. The walls which are nearly perpendicular are formed predominantly of large massive colonies of *Montastrea annularis* some of which are shown on the lower right canyon wall. The shingle-like colonies seen on the upper left hand side are *Porites astreoides*, an important secondary hermatype in this zone. The canyon bottom lies about 8 meters beneath the surface and is covered by sand showing ripple marks. The narrowest part of the canyon is less than one meter wide. The horizontal distance through the center of the figure is about 8 meters.

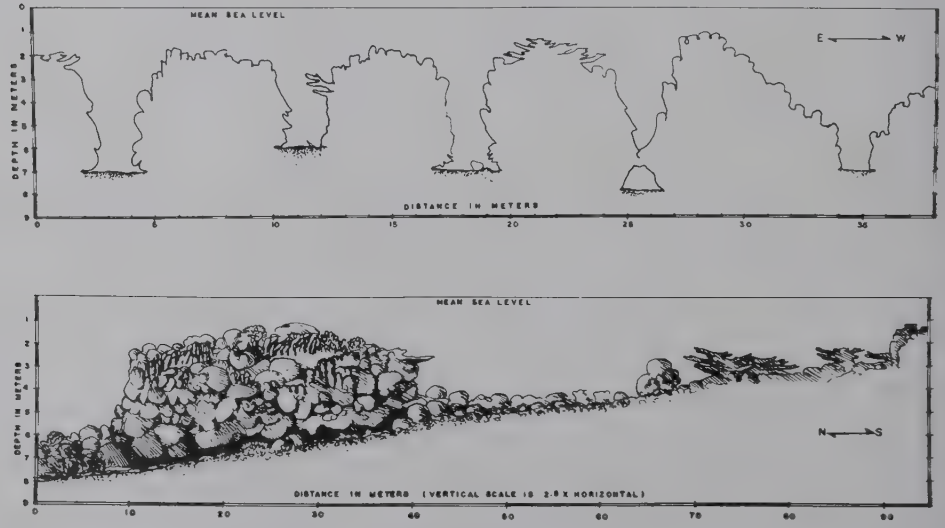


FIGURE 10. Cross sectional and longitudinal transects of the buttress zone in the reef near "Sombra," Ocho Rios. Depths and horizontal distances along the traverse were measured with a sounding line and details filled in from underwater photographs and field sketches. Vigorous growth of coral in the buttresses has resulted in a sharp elevation of these structures above the surrounding sea bottom.

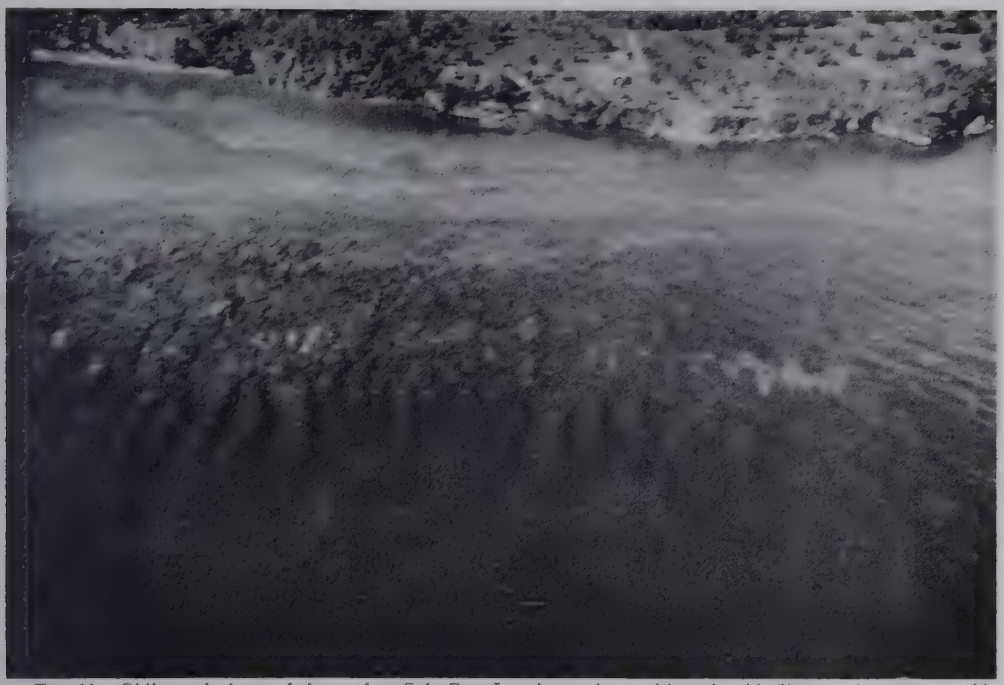


FIG. 11. Oblique airphoto of the reef at Salt Gut, Jamaica, taken with polaroid filter and extreme wide angle lens from a helicopter at an altitude of about 125 feet. In this reef the buttresses are several times larger than they are at Ocho Rios, 10 miles to the west, and the maximum depth of the canyons appears to be about 20 meters. The horizontal distance through the center of the figure is about 200 meters.

heads of *Montastrea annularis, Millepora, Porites porites* and *P. furcata,* and in some places, *Acropora cervicornis* and *A. prolifera.*

The buttress sides are built up primarily by gigantic colonies of *Montastrea annularis* which assume the curious flattened habit shown in the underwater photographs in Figures 14 and 15. *Porites astreoides* is also very common and grows in flattened plate-like colonies the edges of which overlap, giving an appearance of shingles on a roof. Very large colonies of *Colpophyllia natans, Diploria strigosa, D. labyrinthiformis,* and *Dendrogyra cylindrus* are also fairly common (Figure 16). The prevalent zoanthidean in this zone is *Palythoa caribbaea.* Corals which are rare elsewhere on the reef, such as *Madracis asperula, M. decactis, Mycetophyllia lamarckana, Mussa angulosa* and others, become numerous in this zone though they remain unimportant from the point of view of their biomass.

The cervicornis *zone*

The uppermost region of the seaward slope of the fore reef takes its name from the immense beds of staghorn coral, *Acropora cervicornis,* which occur here. The zone is from 30 to 100 meters wide and between 8 and 15 meters deep. It is transected by elongated sandy tracts which are the outward continuations of some of the canyons. The bottom tends to be uneven due to extensive coral growth between the sandy areas. Large colonies of *Montastrea annularis, Porites porites* and *P. furcata* are also abundant, and it is the growth of these corals which appears to initiate the formation of the buttresses in the deeper zones of the seaward slope as seen in Figure 17.

The annularis *zone*

This is the deepest part of the fore reef so far explored. It is characterized by great numbers of multilobar heads of *Montastrea annularis.* Other species as *Diploria labyrinthiformis, D. strigosa, Colpophyllia natans, C. amaranthus, Siderastrea siderea, Porites astreoides, P. porites, Meandrina meandrites, Dendrogyra cylindrus, Dichocoenia stokesii* and various mussids are also more or less abundant and combine to form a rich mixed bottom community. Except for small patches of *Acropora cervicornis,* the Acroporidae are inconspicuous or indeed absent at depths greater than about 15 meters on Jamaican reefs.

Less than 50% of the bottom area of this zone is covered by living coral, and growth is much less vigorous than in the upper zones of the reef.

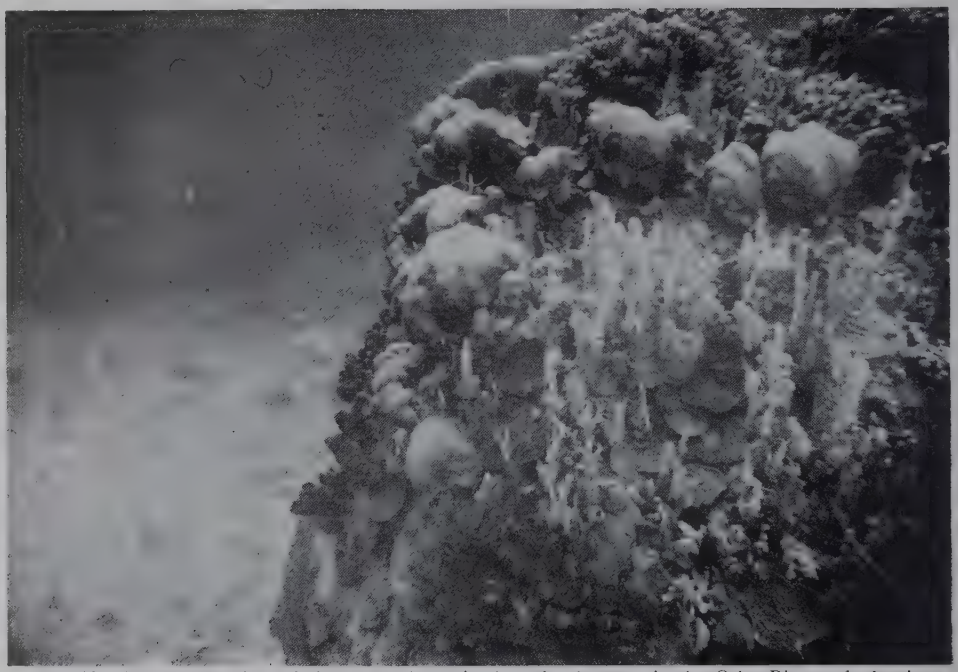


FIG. 12. Underwater view of the seaward termination of a buttress in the Ocho Rios reef, showing a steep promontory projecting outward into much deeper water. The top of this buttress lies 2 meters beneath the surface, the bottom beyond is more than 10 meters deep. The buttress crest bears a large colony of *Porites furcata*, the large coral knobs are *Montastrea annularis*. The flattened growths on the buttress sides are *Millepora alcicornis* and the circular plate-like colonies are *Porites astreoides*. The vertical distance in the middle of the figure is about 6 meters.

It is the writer's impression that both the number and size of the coral colonies per unit area decreases below depths of 20 meters, but this observation must be tentative until more information is available about the deeper regions of the seaward slope.

Zonation in the Port Royal Reefs

The type of zonation described in the preceding section applies in principle to all Jamaican climax reef communities despite the fact that there is considerable variation in the degree of development of the zones in different localities. On the south coast of Jamaica, the largest reefs are to be found between Port Royal and Portland Point. Smaller reefs also exist near the eastern and western ends of the island, and scattered coral growth is frequently found on the bottom even where no true reef communities have become established. Eroded remains of what may once have been extensive reefs can be seen near Morant Bay, Black River and Alligator Pond. Some of these reefs may have been buried by shifting sands and subsequently re-exposed.

Many of the large south-coast reefs in Jamaica show evidence of regression in recent times and there is every indication that the population density in terms of biomass of coral per unit area is lower here than on comparable reefs on the north coast. The most important attributes in which the larger outer reefs near Port Royal differ from the reef at Ocho Rios are: (1) total absence of a buttress zone; (2) very large areas of dead coral in the upper *palmata* zone; (3) a lower population density of acroporid corals in the breaker zone, and (4) the reef crest is more trenched and usually covered with living coral from which *Zoanthus* is practically absent.

It is probable that at least some of these differences are due to the destruction wrought by hurricanes, the most recent of which devastated the southeastern coast of Jamaica in August 1951. The effects of such storms on the population structure of a reef will be discussed below.

The lagoon

South of Port Royal, an area of the shallow offshore shelf about 5 miles wide by 8 miles long

FIG. 13. Underwater view of the landward termination of a large buttress in the Ocho Rios reef, looking backward at the lower *palmata* zone. The height of the buttress wall on the right of the figure is about 4 meters. In the left foreground are some typical mammellate growths of *Montastrea annularis* whereas on the right, this same species shows a flattened colony habit that is characteristic of it when growing on a near vertical surface. The canyon opening out in the middle foreground is partly filled with living coral and detritus, and in the background is a large coral head about 5 meters high composed primarily of *Acropora cervicornis* and crowned with large colonies of *A. palmata*.

has been more or less enclosed by a series of patch and barrier reefs together with their associated cays. The resulting lagoon has an uneven bottom with depths as great as 35 meters and many coral hillocks rising almost to the surface. In its deeper parts, the lagoon floor is covered mostly by calcareous sediments on which living coral growth is incidental or absent.

The large sand and rubble shallows on the western (lee) sides of the cays, are often overgrown with *Thalassia* and *Halimeda*. Here, the small scleractinians such as *Manicina areolata, Porites divericata,* and *Cladocaroa arbuscula* are very common. In somewhat deeper waters, up to 3 meters, *Acropora palmata, Montastrea annularis, M. cavernosa, Porites astreoides, Diploria clivosa, D. strigosa,* and *Acropora cervicornis* and gorgonians are common but they have a patchy distribution. At greater depths, the most important scleractinian is *Montastrea annularis* which forms great multilobar heads that remain separate from each other and show little tendency to aggregate into reefs. In some areas, the bottom is covered with dense growths of *Acropora cervicornis*. The bulk of the fined sediment is made up of *Halimeda* and foraminiferan fragments. The delicate branching coral *Oculina diffusa* is common in the western part of the lagoon where outflowing Kingston Harbour water and muddy bottom provides a somewhat different environment from that found on the reefs.

The reef crest

The barrier reef between South Cay and Southeast Cay, near Port Royal, is about 4 miles long with a crest about 30 meters wide. The maximum depth of the narrow interconnecting channels which cross the area is about a meter and a half, but the tops of the coral colonies are often awash. See Figure 18. In appearance and coral population this region closely resembles the rear zone of the Ocho Rios reef. There is a rich mixed community in which the most prevalent species are *Diploria strigosa, D. clivosa, Montastrea annularis, Porites astreoides, P. porites, Siderastrea siderea, Acropora palmata* and *A. cervicornis,* The Zoanthidea are represented by *Palythoa,* rather than *Zoanthus* which is not common. *Mille-*

FIG. 14. Underwater view of a canyon in the Ocho Rios reef showing the buttress wall covered by very large colonies of *Agaricia agaricites*. This view is in a seaward direction, looking out over the *cervicornis* zone. The canyon shows evidence of being partly filled in through accumulation of coral detritus composed mostly of fragmented *A. palmata* (lower foreground), *A. cervicornis* and *Porites furcata*. Depth of photo is about 4 meters.

pora alcicornis exists in this zone as rather small encrusting colonies. In many places the reef crest is replaced by shingle ramparts which in some cases have grown large enough to form islands or cays able to support land plants such as Mangrove, *Ipomea* and *Sesuvium*. There is no well defined rear zone; instead, the reef crest merges gradually with the lagoon and the number of corals becomes progressively smaller until only a few hardy specimens of *Porites astreoides, Diploria clivosa, Favia fragum* and *Siderastrea radians* remain in the shallow sand flats.

The breaker zone

The breaker zone of the main barrier reef that forms the southern boundary of the Port Royal tract has an atypical appearance because the elkhorn coral *Acropora palmata* does not achieve the spectacular growth that is so characteristic of it on the north coast reefs. This zone is in many places severely damaged and the bottom is strewn with dead, broken and and overturned colonies, as seen in Figure 19. *Acropora palmata* is still very common, but it no longer enjoys the dominant position that it does on other reefs. To some extent it has been replaced by *Diploria strigosa*, a massive "brain coral" which grows to very large sizes here (see Figure 20). *Millepora* is another hermatype which has taken advantage of the lack of competition. This is more abundant than *Acropora palmata* in many localities, and forms great flattened heads about 5 meters long and 4 high, as shown in Figure 21. The tops of these formations are usually awash and often exposed at low tide. In many cases the uppermost parts of these heads are dead and overgrown by a veneer of *Lithothamnion*. On the eastern windward sides of Southeast Cay, Maiden Cay and Gun Cay, large groups of *Millepora* colonies coalesce to form true hydrozoan reefs.

As a result of these observations we believe that the somewhat anomalous population structure of this reef zone may be due to disruption of normal reef growth processes by severe storms, or, less likely, by the great earthquakes which destroyed nearby Port Royal in 1692 and Kingston in 1907. Whatever the cause, the presence of enormous amounts of *Acropora palmata* shingle, together with the fact that there is a comparatively reduced population of living acroporids over large parts of this zone at the present time, may be taken as evidence that this reef has been more productive in the recent past.

The seaward slope

In these reefs, which lack the buttress zone, the *palmata* zone is part of the fore reef. As indicated by the great masses of *Acropora* rubble which cover about 80% of the bottom, there has been severe damage and little living coral remains down to depths of approximately 6 meters. However, in isolated localities, where the coral has escaped destruction, the normal ecological structure of the reef is preserved and there are very rich populations of *Acropora palmata* which resemble those seen on the north coast. Other cases of extensive coral destruction have been noted by Steers *et al.* (1940) on several days in Portland Bight, and by Zans (1957b) on the Pedro Cays. The recolonization of the denuded areas by coral seems to be slow, presumably due to the instability of the unconsolidated shingle. Hence much of this region is a submarine desert in comparison to the corresponding zone of the Ocho Rios reef.

FIG. 15. Horizontal underwater view into a canyon in the Ocho Rios reef. The depth at which the photo was taken is about 9 meters. Here the canyon is floored by fine sand. The buttress wall on the right is composed of a single gigantic colony of *Montastrea annularis* which has assumed a flattened shingle-like habit, resembling flow sheets. The vertical distance covered by the middle of the figure is about 4 meters.

The deeper parts of the fore reef have typical *cervicornis* and *annularis* zones which differ from those on the north coast only in that there is rather less vigorous growth of coral and larger sandy areas which contain no coral at all.

DISCUSSION

The distribution of shallow water Scleractinia in the Caribbean area

The Caribbean area is remarkably homogeneous with regard to the shallow-water Scleractinia. There are no important regional differences in the reef coral populations and no corals have yet been found that are peculiar to any one locality. Even in the case of Bermuda, which lacks four families and twelve species, there are no shallow-water corals which are not commonly found elsewhere in the Caribbean area. This fact is demonstrated in Table IV which compares the known scleractinian fauna of Jamaica (41 species) with that of Florida (42 species), Bahamas (37 species), Barbados (26 species) and Bermuda (19 species). The variation of the species number in the first three localities is almost certainly due to the vagaries of "collector's luck" rather than to any significant faunistic differences, whereas the list of Barbadian species is probably still incomplete and no conclusions can be drawn. Bermuda, on the other hand, definitely lacks the Acroporidae, the Meandrinidae, the Dendrophylliidae and the Caryophylliidae, as well as many of the Faviidae, Poritidae and others.

Vaughan and Wells (1943 pp. 76-77) stated that the Bahamas had more species of hermatypic corals than any other locality in the West Indies. However, it is clear from more recent evidence (cf. Smith 1948, and this paper) that a species maximum may exist in that part of the Caribbean delineated roughly by Florida and the Bahamas in the north, the Isle of Pines in the west, and Jamaica and Puerto Rico in the south. However, far too little accurate information is at present available on the distribution of hermatypic corals in the West Indies to define with any exactitude the limits of such a coral population center. A careful survey is required in which special attention is paid to the peripheral islands, for example Anegada, Barbuda, Guadeloupe, Barbados, Tobago, Curacao and Bonaire, and to the reefs of the San Blas Archipelago in Panama, the Mosquito Cays near Nicaragua, Cozumel Island and Vera Cruz (see Heilprin 1890) in Mexico. Reliable check lists of the reef building corals should also

FIG. 16. Underwater view of the region where the buttress and *cervicornis* zones merge. The latter is seen in the background. In the foreground is a very large colony of *Dendrogyra cylindrus* growing at the outer foot of a buttress in the Ocho Rios reef. The depth of the great thicket of *Acropora cervicornis* in the background is about 10 meters.

be compiled for Cuba, Hispaniola, Puerto Rico, and the Virgin Islands. Thus, rather than to answer questions, the present study can only serve to point out the necessary steps to be taken in solving the problem of the origin and distribution of the Caribbean reef coral populations.

Growth and zonation of an offshore reef

The accumulation of calcareous matter by corals and other hermatypes to form a reef depends on 2 important factors. First, the overall rate of deposition must exceed the rate of erosion from all causes. Second, a suitable framework consisting of large coral or algal blocks must be formed in which finer detritus can accumulate and consolidate.

Given optimum conditions for growth the total transfer rate of calcium carbonate by hermatypes into the reef depends on the biomass of the various species, their growth rate, the resistance of their skeletons to erosion and translocation, and the speed with which the skeletal material is finally consolidated into the permanent structure of the reef. Whether a dead coral colony is buried *in situ* into the reef framework or whether it is first broken up, disintegrated and transported away to become a part of the unconsolidated sediments of the fore reef and lagoon is determined by such factors as the size and shape of the colony, *e.g.*, large or small, massive or branching, its hardness and the degree of exposure to heavy seas and other forms of mechanical or chemical attrition.

The question of whether there is a single most important coral species from the point of view the bulk of calcareous material it contributes to the framework of the reef is an interesting one. Ginsburg (1956) sums up the prevalent notion in his recent paper to the effect that elkhorn coral *Acropora palmata* is the primary structural element of Floridian reefs, providing a framework in which detrital material can accumulate.

Since the shallow zones of the reef described above are as a rule dominated by the great branching growths of *Acropora palmata*, and since fragmented colonies of this coral form the bulk of the calcareous detritus thrown up on the shingle ramparts, it is natural to conclude on the basis of superficial examination that this species might therefore also be the primary hermatype of Jamaican reefs. However, our observations on these reefs indicate that *Acropora palmata* is restricted almost entirely to the zones in the upper six

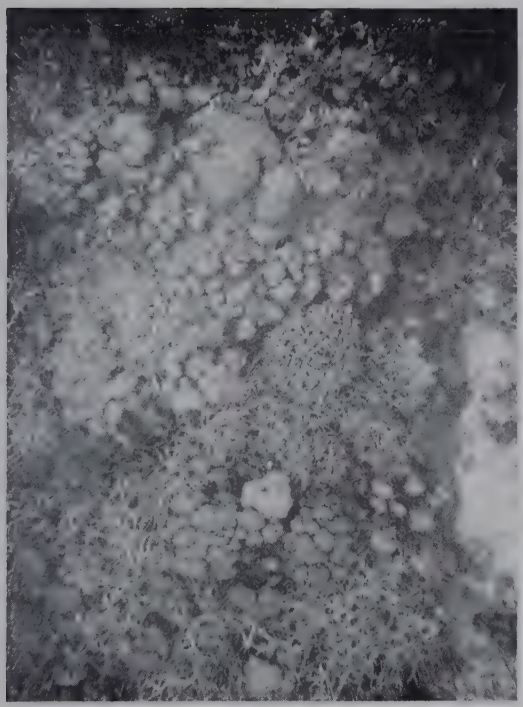


FIG. 17. Vertical underwater view of the junction between the buttress and *cervicornis* zones, showing the characteristically rich growth of coral in this region. The massive coral is *Montastrea annularis*, the blunt branched coral in the center is *Porites furcata*. A large bed of staghorn coral *A. cervicornis* grows in the space between the more massive corals. The *cervicornis* zone starts on the left of the figure. The sandy strip running across the bottom is a canyon debouching from the buttress zone. The depth is about 8 meters.

meters of the reef habitat, and that the most vigorous proliferation occurs not in the *palmata* zone but in the buttress zone where enormous colonies of *Montastrea annularis* make up the greater part of the calcareous material of which the reef is composed. It is interesting to note in this connection that *Montastrea* sp. is also by far the commonest and often the only fossil framework coral to be found in exposures of the Pliocene and more recent coastal reef limestones of northern Jamaica.

The extensive proliferation of *Acropora palmata* that is so characteristic of the upper zones of West Indian reefs probably indicates a reef community in the later stages of development. To provide the shallow conditions necessary for the growth of this coral however, a suitable platform must first be formed; in many cases this is accomplished by the activities of other coral species. In Jamaican reefs, the broad base of the reef is formed predominantly by *Montastrea annularis*, with such branching species as *Porites furcata* and *Acropora cervicornis* providing most of the finer detritus that fills the crevices between the colonies

TABLE IV. Geographic distribution of West Indian shallow water corals*

Family and Species[1,2]	Jamaica[3,4,5]	Florida[6,7]	Bahamas[6,7]	Barbados[8,9,10]	Bermuda[7,11]
ASTROCOENIIDAE					
A. pectinata	–	+			
S. michelinii	+	+	+	+	+
ACROPORIDAE					
A. cervicornis	+	+	+	+	–
A. palmata	+	+	+	+	–
A. prolifera	+	+	+	–	–
POCILLOPORIDAE					
M. decactis	+	+	+	+	+
M. asperula	+	–		+	–
AGARICIIDAE					
A. agaricites	+	+	+	–	–
A. fragilis	+	+		+	+
A. nobilis	+	+	+	–	–
SIDERASTREIDAE					
S. radians	+	+	+	+	+
S. siderea	+	+	+	+	+
PORITIDAE					
P. astreoides	+	+	+	+	+
P. branneri	–	–	+	–	–
P. divaricata	+	+	–	–	–
P. furcata	+	+	+	–	–
P. porites	+	+	+	+	+
FAVIIDAE					
F. fragum	+	+	+	+	+
D. clivosa	+	+	+	+	–
D. strigosa	+	+	+	+	+
D. labyrinthiformis	+	+	+	+	+
C. amaranthus	+	+	+	–	–
C. natans	+	+	+	+	–
M. areolata	+	+	+	–	–
M. mayori	–	+	–	–	–
C. arbuscula	+	+	+	–	–
S. bournoni	–	+	+	–	–
S. hyades	+	+	–	–	–
M. annularis	+	+	+	+	+
M. cavernosa	+	+	+	+	+
RHIZANGIIDAE					
A. solitaria	+	+	+	+	+
P. americana	+	+	–	–	–
OCULINIDAE					
O. diffusa	+	+	+	–	+
O. valenciennesi	+(?)	–	+	–	+
O. varicosa	–	+	–	+	+
MEANDRINIDAE					
M. meandrites	+	+	+	–	–
M. braziliensis	+	+	+	+	–
D. stokesi	+	+	+	+	–
D. cylindrus	+	+	+	+	–
MUSSIDAE					
M. angulosa	+	+	+	+	–
I. rigida	+	+	+	–	+
I. multiflora	+	+	+	+	+
I. sinuosa	+	+	+	–	+
M. lamarckana	+	+	+	+	–
CARYOPHYLLIIDAE					
E. fastigiata	+	+	+	+	–
DENDROPHYLLIIDAE					
T. tenuilamellosa	+	–	–	–	–
Total species	41	42	37	26	19

*[1] Vaughan and Wells (1943)
[2] Wells (1956)
[3] Goreau (1956)
[4] Duerden (1902)
[5] Fontaine (1954)
[6] Vaughan (1910 et seq.)
[7] Smith (1948)
[8] Goreau (unpublished field notes)
[9] Butch (1939)
[10] Nutting (1919)
[11] Verrill (1901b)

FIG. 18. Underwater view of the reef crest of the barrier reef near South Cay, Port Royal, Jamaica, looking toward the breaker zone. The dominant coral in this region is *Diploria strigosa* which forms the large hemispheroidal brain coral colonies in the foreground. Each of these is about one meter in diameter. In the middle background is a colony of *Acropora palmata*. The depth is about two meters.

of the massive framework corals. Once it becomes established however, *Acropora palmata* quickly builds up the crest of the reef by virtue of its known fast growth (Vaughan 1915b) and the great fragility of its skeleton. This leads to the formation of extensive shallow flats such as are seen in the Ocho Rios reef where the dead coral is overgrown by *Zoanthus sociatus*. It also contributes extensively to the formation of large shingle ramparts and islands through the piling up of wave transported *palmata* rubble.

The formation of buttresses raises some important questions about the past history of Jamaican reefs. The main problem is whether the buttresses are constructional or erosional in origin.

Tracey *et al.* (1948) have described spur and groove systems formed by the profuse growth of hermatypic calcareous algae in the windward reefs of Bikini and other atolls in the Marshall Islands. These authors stated that the floor of the grooves represents an older surface upon which the algal spurs have grown. Newell *et al.* (1951) described complicated submarine trenches in shallow water on the northeastern coast of Andros Island, Bahamas. Coral and calcareous algae are sparse here and have no influence on the shape of the grooves which are believed by these authors to be caused by erosion of the underlying limestone (oölite) surface by undertows generated during storms.

In Jamaican reefs the buttress zone is formed by the vigorous proliferation of massive corals. Buttresses may develop in those regions of the reef where rapid coral growth can occur both upward toward the light and outward into the prevailing seas. Nearly all stages of the differentiation of buttresses can be observed in certain parts of the fore reef at Ochos Rios and elsewhere on the Jamaican north coast. The first step seems to be the formation on the fore reef of coral hillocks which are principally composed of one or more large heads of *Montastrea annularis*. Concomitant with an increase in height is the elongation of the coral heads by forward growth to form spurs which are oriented in a direction normal to the reef front, i.e., into the prevailing seas. Due to lateral growth, the sandy spaces between the spurs become gradually narrower until true canyons are formed with their characteristic vertical or overhanging walls. Further encroachment results in roofing over and eventual obliteration of the can-

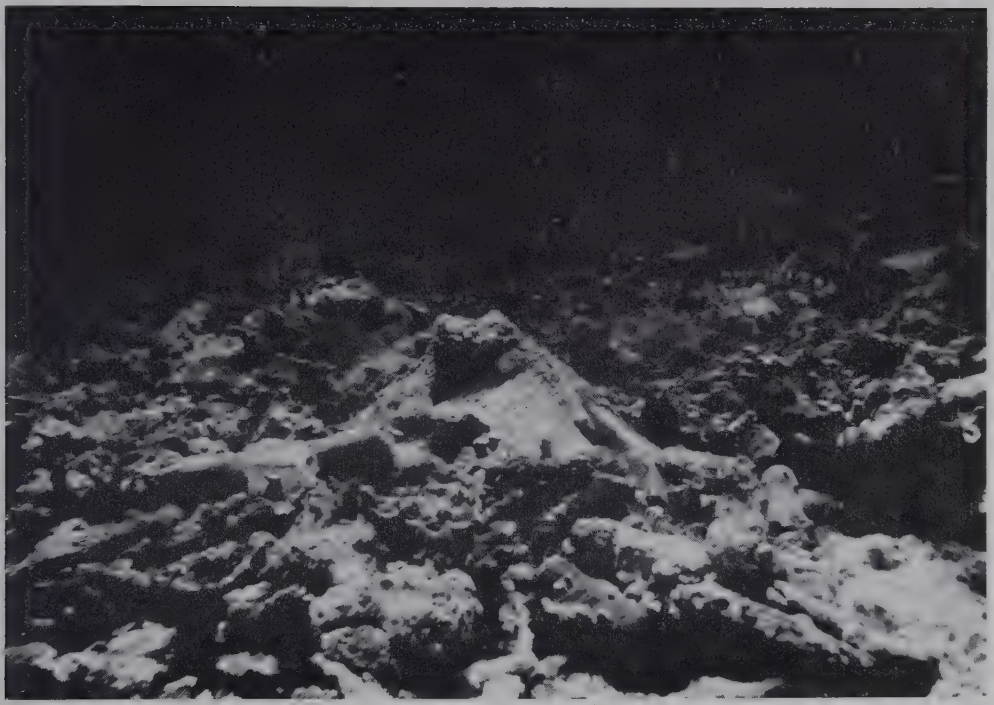


FIG. 19. Destruction of the breaker zone in the barrier reef near South-East Cay, Port Royal, possibly by the hurricane of 17 August 1951. Large overturned colonies of *Ocropora palmata*, such as those seen in this figure, occur everywhere, and in some there is an attempt at regeneration. The depth is about 2 meters.

vons. In certain parts of the reef west of Ocho Rios, many of the canyons were observed to be partially filled with detritus composed mainly of dead fragments of *Acropora palmata* which was derived from the numerous colonies of this coral that were seen growing on the tops of the buttresses in this region. By virtue of their location at the juncture of the reef crest with the fore reef, the canyons are ideal chutes which facilitate the drainage of sediment from the turbulent zones at the upper reef into deeper water by undertows set up in the breaker zone. There is no evidence that this process results in undercutting or deepening of the trenches through erosion since all the available surface area of the canyon walls is covered by living coral and is thus protected against scour.

A structure superficially reminiscent of the "room and pillar" formation described by Tracey *et al.* (1948) on the Bikini reefs was observed in Jamaica by the writer from a helicopter on the eastern side of Oracabessa harbor where the reef is protected from the prevailing seas by a promontory. Here the outer reef, corresponding to the buttress zone, is composed of huge coral bosses ranging in size from about 2 to 10 meters across and having the appearance of irregular polygons separated from each other by narrow deep rifts. Much less well defined but basically similar patterns were also seen from the air in the great reef buttress near Boscobel, Jamaica. Unfortunately, these interesting features have not as yet been explored underwater and we are unable to give any information about the nature of the coral growth in these localities.

The possibility has been considered that the buttresses may be due to secondary growth of coral on submerged cliffs previously dissected by subaerial erosion during a period of emergence. This is held to be unlikely for two reasons: first, buttresses are seen in all stages of growth and differentiation on the fore reef at the present time; and second, the geological record shows that the north coast of Jamaica has been uplifted, rather than submerged, in Pleistocene times. It is therefore likely that the buttresses are to be regarded as a growth form of a reef in a youthful and vigorous stage of its development. Nevertheless, the final answer to this intriguing question is still in the offing and waits the outcome of further investigations now planned or in progress.

SUMMARY AND CONCLUSIONS

1. Jamaica has 41 known species of shallow water Scleractinia belonging to 25 genera and 13

FIG. 20. Underwater view of the breaker zone in the Port Royal barrier reef near South Cay. The relative scarcity of *Acropora palmata* in this region is evident, the commonest coral being *Diploria strigosa* a brain coral, large hemispherical colonies of which are seen in the middle of the photo. A large head of *Millepora alcicornis* appears in the distant background. Much dead coral is seen on the bottom in the right foreground where the depth is about 3 meters.

families. Of these all except 5 species are classified as hermatypic corals.

2. The larger reefs of Jamaica are of the fringing barrier type with scleractinians as the most important hermatypic organisms. Profile traverses carried out on mature reefs demonstrate the existence of three main regions: the back reef, reef crest, and seaward slope. These in turn are divided into 7 to 9 different zones named according to their most important faunal or structural features. Going shoreward from deep water these zones are: (1) the *annularis* zone, (2) the *cervicornis* zone, (3) the buttress zone, (4) the lower *palmata* zone, (5) the upper *palmata* or breaker zone, (6) the reef flat, (7) the rear zone, (8) the channel or lagoon zone, (9) the inshore zone.

3. Observations on two representative reefs, one on the north coast and one on the south coast of Jamaica, show that zone structure and species succession is fundamentally similar in the two cases. In view of the great destruction and other changes observed on several reefs in the south coast of Jamaica it is considered likely that storms can play an important part in altering the basic pattern of species dominance and zonal succession in the upper parts of a climax reef.

4. Evidence is presented to show that *Montastrea annularis* forms the broad basis of the reef and that it is the single most important framework coral in Jamaican reefs. Colonies of this massive species grow to very large size in the seaward slope, notably in the buttress zone. In shallower water, *Acropora palmata* becomes the dominant coral. This species is important because of its abundance and the relative ease with which its colonies are broken up by heavy seas, thus readily providing the great quantities of detrital material with which the reef flat and ramparts are built up.

5. The spurs of the buttress zone are probably formed through the coalescence of large heads of *Montastrea annularis* and other massive corals. The sandy crevices between the buttresses are gradually narrowed by lateral growth of coral to form canyons. As such, the canyons probably facilitate the movement of sediments from the turbulent upper zones into the deeper regions of the fore reef. The canyons tend to be obliterated

FIG. 21. Underwater view of the breaker zone of the Port Royal barrier reef near South Cay where the dominant hermatype is the hydrocoralline *Millepora alcicornis*. Very large colonies of this appear in the right background. *Acropora palmata* and a large massive *Diploria strigosa* are seen in the foreground. The depth is about 3 meters.

by a combination of overgrowth and filling in by coral broken away from the crests of the buttresses.

REFERENCES

Browne, Patrick. 1756. Civil and natural history of Jamaica. London.

Butch, R. S. 1939. The reef corals of Barbados. J. Barbados Museum and Natural History Society VI, No. 3.

Duerden, J. E. 1902. West Indian madreporarian polyps. National Acad. Sci. Mem. **7**: 403.

Emery, K. O., J. I. Tracey and H. S. Ladd. 1954. Geology of Bikini and nearby atolls. Part I. Geology. U. S. Geological Survey Professional Paper 260-A, pp. 1-265.

Fontaine, A. R. 1954. Notes on the marine invertebrate collections: Corals. Inst. Jamaica Ann. Rep. 1953-1954, pp. 24-25.

Ginsburg, R. N. 1956. Environmental relationships of grain size and constituent particles in some south Florida carbonate sediments. Bull. Amer. Petrol. Geol. **40**: 2384-2427.

Goreau, T. F. 1956. On the biology and histochemistry of corals. Ph.D. thesis, Yale University.

Heilprin, A. 1890. The corals and coral reefs of the waters of the Gulf of Mexico. Acad. Nat. Sci. Phila. Proc. **42**: 303-316.

Johnson, J. H. 1954. Fossil calcareous algae from Bikini Atoll. Bikini and Nearby Atolls. Part 4, Paleontology. U. S. Geoglogical Survey Professional Paper 260-M, pp. 537-545.

Nutting, C. C. 1919. The Barbados Antigua Expedition. Narrative and preliminary report. Univ. Iowa Stud. Nat. Hist. **8**: 1-274.

Newell, N. D., J. K. Rigby, A. J. Whiteman and J. S. Bradly. 1951. Shoal water geology and environments, eastern Andros Island, Bahamas. Bull Amer. Mus. Nat. Hist. **91**: 1-30.

Pilsbury, R. K. 1951. An analysis of surface wind observations at Palisadoes Airport and Montego Bay Airport. The Jamaica Government Printer.

Sloane, Hans. 1707. A voyage to the islands of Madeira, Barbados, Nevis, St. Christopher's and Jamaica, together with a natural history of the last of those islands. Vol. I. London.

Smith, F. W. Walton. 1948. Atlantic Reef Corals. University of Miami Press.

Steers, J. A., V. J. Chapman, J. Colman and J. A. Lofthouse. 1940. Sand Cays and Mangroves in Jamaica. Geogr. J. **96**: 305-328.

Tracey, J. I., H. S. Ladd and J. E. Hoffmeister. 1948. Reefs of Bikini, Marshall Islands. Bull. Geol. Soc. Amer. **59**: 861-878.

Vaughan, T. W. 1910. The recent madreporaria of southern Florida. Yearb. Carnegie Inst. Wash. **8**: 135-141.

———. 1911. Recent madreporaria from southern Florida. Yearb. Carnegie Inst. Wash. **9**: 135-144.

———. 1912. Madreporaria and marine bottom de-

posits of Florida. Yearb. Carnegie Inst. Wash. 10: 147-156.

———. 1913. Study of the geology and the madreporaria of the Bahamas and southern Florida. Yearb. Carnegie Inst. Wash. 11: 153-162.

———. 1914. Reef corals of the Bahamas and southern Florida. Yearb. Carnegie Inst. Wash. 13: 222-233.

———. 1915a. On the recent madreporaria of Florida and the West Indies. Yearb. Carnegie. Inst. Wash. 14: 220-231.

———. 1915b. The geologic significance of the growth rate of the Floridian and Bahamian shoal water corals. J. Wash. Acad. Sci. 5: 591-600.

———, **and J. W. Wells.** 1943. Revision of the suborders, families and genera of the scleractinia. Geol. Soc. Amer. Spec. Pap. No. 44.

Verrill, A. E. 1901a. Variations and nomenclature of Bermudian, West Indian and Brazilian reef corals with notes on various Indo-Pacific corals. Trans. Conn. Acad. Arts. Sci. 11: 63-168.

———. 1901b. Comparisons of the Bermudian, West Indian and Brazilian coral faunae. Trans. Conn. Acad. Arts Sci. 11: 170-260.

Wells, J. W. 1951. The coral reefs of Arno Atoll, Marshall Islands. Atoll Res. Bull. No. 9.

———. 1954. Recent corals of the Marshall Islands. Bikini and Nearby Atolls. Part 2, Oceanography (Biologic). U. S. Geological Survey Professional Paper 260-I, pp. 385-486.

———. 1956. The Scleractinia. Treatise on Invertebrate Paleontology. Part F, Coelenterata, pp. 328-444. The Geological Society of America and University of Kansas Press.

Zans, V. A. 1957. Pedro Cays and Pedro Bank. Report on the survey of the Cays 1955-1957. In press.

AN ANALYSIS OF LEARNING IN YOUNG ANATIDAE[1]

PETER H. KLOPFER
Zoology Department, Yale University[2]

IMPRINTING AND DETERMINATION OF SPECIES-SPECIFIC BEHAVIOR

Whatever the processes involved, the young of any species must in some way come to respond appropriately to the behavior patterns characteristic of their own species if they are to reproduce successfully, while, at the same time, selective pressures maintain inter-specific differences in these patterns. In the case of extremely precocial forms like the megapodes, where incubation is by means of solar or organic heat (Frith 1956), species-specific behavior cannot be learned by the young through a physically enforced association with their parents. Conversely, a young thrush, confined by its physical condition to a nest and fully dependent upon parental care, is in a position to make ample use of conventional associative processes.

There are numerous intermediate situations. In most ducks and geese, while there may be a considerable degree of parental care, the young are nonetheless physically able to disperse several hours after hatching. Whatever bond exists to hold the young to their parents must either be present at hatching or developed within this short period. Spalding (1954), in a paper that escaped general notice until recently, described the behavior of newly hatched chickens, which tended to follow whatever moving object they first saw upon hatching. Heinroth (1910), and later Lorenz (1935), worked out details of this following-reaction, showing that the object followed formed the basis of the young's subsequent choice of a parent-*Kumpan,* and, in some instances, sex-partner. This process, which has been subjected to more quantitative studies (Jaynes 1956, Ramsay and Hess 1954, Hinde *et al.* 1956), was termed imprinting (*Prägung*), and was defined by Thorpe (1951) as follows:

> "A rapid and stable form of learning taking place early in the life of social species, whereby, often apparently without immediate reinforcement, broad supra-individual characteristics of the species come to be recognized and used as releasers."

Some workers feel that this process is not to be differentiated from a form of simple conditioning (Hinde *et al.* 1956, Fabricius 1951a), a view with which Thorpe (1956 pp. 115-118) now concurs. This view is supported by evidence that imprinting is not always as stable or irreversible as Lorenz's early papers indicated (*cf.* Stevens 1955 for an example), but certain differences from other learning processes do remain. First, imprinting is restricted to specific "critical" periods of the organism's life (*cf.* Scott and Marston 1950). Second, the reenforcement, such as it is, lies in a reafference effect, *i.e.,* the more the animal must exert itself in following a model, the more firm the bond to that model (Hess 1955). However, a final statement must await the time

[1] A portion of a dissertation presented to the faculty of Yale University in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

2. Present address: Zoology Department, Duke University, Durham, N. C.

when a great deal more information about imprinting is available.

What seems most likely is that imprinting will be shown to represent a segment along a continuum, one end of which represents behavior directly determined by morphologic features (as in animals with specialized feeding apparatus) while the other end represents more plastic categories determined over a longer interval of the animal's life. In phylogeny, as Thorpe (1956), Ewer (1956) and Pringle (1950) have also suggested, the position of certain acts can be shifted along the continuum. That is, acts which were once learned by a juvenile or mature animal can be replaced by functionally similar acts which are "learned" before birth. Such a replacement of a phenotypic by a genotypic character is fully consistent with modern evolutionary theories. The proportion of an animal's acts which falls on any portion of the continuum may be a function of the lability of its environment, its degree of motor precocity, and, possibly, the total amount of neural material available (*cf.* Fankhauser 1955, and Vernon and Butschi 1957). Imprinting, then, represents an intermediate segment and is of particular advantage to animals in which locomotor development is well advanced at birth.

Avian Sound-Signals

The present study is primarily concerned with an analysis of the manner whereby certain birds come to know the calls characteristic of their species. These calls are often highly characteristic of a particular species or situation. Frings (1955), for example, has reported on the feeding-releasing value of a particular call by *Larus argentatus,* the herring gull. The species considered here, various ducks and geese, are nidifugous, a characteristic which appears to be phylogenetically older than the nidicolous situation. Presumably there has been a progressive shortening of the incubation period, with concommitant metabolic changes (Howard 1947, 1950, Holmgren 1955, Kendeigh 1952). Considering the conservative nature of bird behavior, valuable insights into the evolution of behavior could be gained by a comparison of the learning mechanisms of nidifugous and nidicolous birds. In this connection it is useful to recall that display characteristics in the Anatidae are of so conservative a nature as to have furnished a more reliable taxonomic guide than certain formerly-used morphologic features (Heinroth 1910, Lorenz 1941). Petrunkevitch (1926) found a similar situation in certain spiders.

The role of different processes in the learning of sound-signals is still far from clear for the majority of avian species. Recently there has been a resurgence of interest in the study of passerine song and its mode of development. Relevant data are contained in the papers of Marler (1952, 1955, 1956a, 1956b), Messmer and Messmer (1956), Metfessel (1935), Poulsen (1951), Sauer (1955) and Thorpe (1956). As yet, too few species have been studied to give a complete picture, but the differences among species that have been studied are considerable. Some, like the common roller canary, *Serinus canarius,* and whitethroat, *Sylvia communis,* produce normal song even when reared in complete auditory isolation (Metfessel 1935, Sauer 1955). In the chaffinch, *Fringilla coelebs,* Poulsen (1951) reports that a predisposition to learn the correct song exists during the bird's first spring. Thereafter, if the bird has been isolated from other birds, there is no apparent preference for particular series of sounds. In this species (unlike the canary) male gonadal hormones will not enable a female to produce male song. A more intensive study of the chaffinch by Thorpe (1956) suggests that certain components of the song are acquired by means of a rapid form of learning akin to imprinting, that others are acquired by a more gradual learning process, and that certain features such as song-duration are innate. Similar variations exist with regard to call notes. Unfortunately it is not always clear what an author means by "reared in isolation." Hatching and hand-rearing young passerines are extremely difficult, although some workers have achieved a notable success. What seems often to be the case, though it is not always stated, is that the birds are taken from the nest after pipping, or even after attaining several days of age. Since Simms (1955) has claimed to have recorded a series of calls and responses between a brooding stone curlew, *Burhinus oedicnemus,* and its unpipped young the validity of this procedure is open to question. External influences may be operative earlier than has been suspected.

In non-passerine birds, where signals are usually less complex musically, the situation has not yet been carefully examined. Collias and Joos (1953) have analyzed spectrographically the calls of domestic hens, *Gallus gallus.* Others (Collias and Collias 1956, Ramsay and Hess 1954, and especially Fabricius 1951a, 1951b) have made incidental observations on the role and specificity of sound-signals. There had been some disagreement as to the functions of the vocalizations of female ducks leading young, Lorenz (personal communication) having stated that it is necessary for anyone wishing to release following among young mallards to imitate accurately the female

mallard's quack. This has not been the experience of others, including myself, who have found that often no vocalizations at all are required and that the crudest imitation will suffice so long as the sounds are short and repetitive. Fabricius (1951a) found that his ducks, which were reared in full isolation, would approach such a sound when enclosed in a box from which the source of the sound was not visible. Ramsay and Hess (1954) were not successful in teaching their mallards to approach a particular sound (recorded mallard quacks) by exposing them to that sound before pipping. When it was emitted by a fully visible model duck the sound was effective, in that the birds subsequently approached that particular model in preference to another. The small number of ducks used and the great variability shown by them throws some question on the significance of these data. Using a larger group, however, they were able to show the absence of consistent innate preferences for particular sounds. Fabricius (1951a and personal communication) suggests that the behavior of different ducks may be related to their habitat preferences. For example, tufted ducks, *Aythya fuligula,* which frequent heavily overgrown shorelines, are far more vocal than the more oceanic eider, *Somateria mollisima.*

In this study we are specifically concerned with these questions:

1. What are the conditions under which young ducks and geese come to respond to particular auditory stimuli?
2. How do these conditions vary in groups with different ecologic status?
3. How do social interactions within clutches influence these conditions?

Methods

In addition to observations made on normally reared birds, which served as the basis for the classification of responses given below, the ducklings were divided into these groups:

1. Isolates, which never saw the experimenter or heard any of the sound-signals used.
2. Sound Only, which were periodically exposed to one particular sound-signal of 3 minutes duration for 10 hours after hatching. The total period of exposure was 30 minutes.
3. Sound with E, which followed the experimenter while being exposed to one particular sound-signal as soon as they were able to walk. The birds were exposed at intervals for a total of 30 minutes.

These conditions, it should be noted, correspond to the various conditions which prevail in the wild. Hole-nesting species, like the woodduck, must respond to auditory stimuli before having had an opportunity to follow visual stimuli. The young are hatched inside recessed holes in trees and emerge for the first time in response to the calls of their mother when she is situated outside the nesting hole (Forbush 1925, Morrill, personal communication and film). The young of surface-nesting species like the mallard, on the other hand, are able to see their mother move away at the time they first begin to follow her and respond to her vocalizations (Collias and Collias 1956). It is possible, therefore, to believe that while the woodduck must be able to learn responses to certain calls before having followed a visual pattern, the mallard has the opportunity to learn similar responses to auditory signals in a more gradual fashion. The tendency of newly hatched precocial birds to follow moving objects has already been well established (Ramsay and Hess 1954, Hess 1955, Fabricius 1951a, Lorenz 1935, Nice 1953, Jaynes 1956).

Newly hatched young of the following species were used:

Surface nesters:

Branta canadensis	Canada goose
Anser canagicus	Emperor goose
Anser rossi	Ross goose
Anas acuta	Pintail duck
Anas platyrhynchos	Mallard duck
Anas strepera	Gadwall duck
Anas silbatrix	Chiloe widgeon
Anas discors	Bluewing Teal
Aythya americana	Redhead duck

Hole nester:

Aix sponsa	Woodduck

others:

Cairina moschata	domestic Muscovy duck

Hatching of the eggs took place in an incubator insulated from any but the loudest noises, apart from the hum produced by the ventilating system. In all cases, birds were hatched in groups of two or more in order to maintain normal sibling relations.

Age of the birds, measured from the time of total emergence, was determined to the nearest hour when hatching occurred during the day. Less accuracy was possible for hatchings which occurred between 11 p.m. and 7 a.m., although, the time required for complete drying in each incubator being known, it was possible to gauge the age of birds that hatched between 4 a.m. and 8 a.m. to within two hours. The variance for birds hatching between 12 midnight and 4 a.m.

was somewhat greater, but hatchings at these hours were fortunately rare.

About 12 hours after exposure to either the experimenter and sound or to sound alone, or, in the case of Isolates, at age 18 to 24 hours, the birds were introduced, singly, into the testing apparatus (Figure 1) and their responses to 7 different sound-signals noted. When placed in a semi-darkened room and illuminated from beneath the screen, this box made it possible to observe the ducklings without their being disturbed by the presence of an observer.

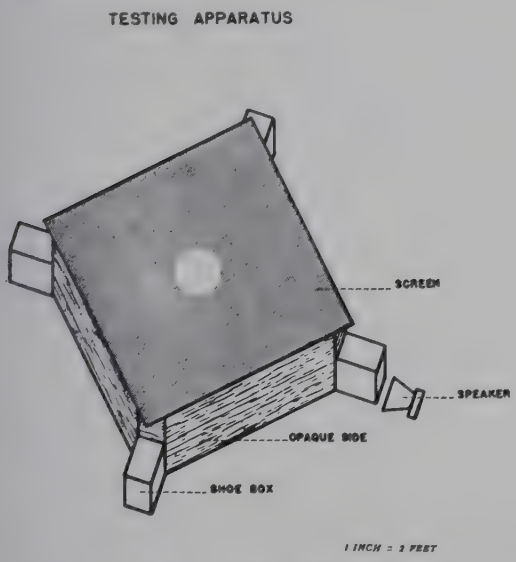


FIG. 1. Testing apparatus.

The sounds were reproduced on a VM tape recorder with the volume level adjusted so as to maintain a reasonably constant output.

Ducklings were transferred directly from their incubator to the center of the testing apparatus. After a pause of from 30 to 60 seconds, a sound-signal, the source of which was adjacent to one of the shoe boxes was introduced and the response of the duckling recorded. Each of the 7 sound-signals had a duration of 3 minutes.

In the tests, a series consisted of a sequence of sound-signals presented one after the other. A trial refers to a single presentation of a sound-signal of 3 minutes duration during the course of a series. Occasionally, for the reasons given below, there were pauses of from 1 to 5 minutes between consecutive trials. The position of the sound source was randomly altered from trial to trial and the sequence of trials was also altered from one series to the next. This latter measure actually proved unnecessary, for, so long as a series did not last more than 20 to 30 minutes, most ducklings showed no changes in response tendencies due to fatigue.

Upon being introduced into the testing apparatus, the birds, depending somewhat upon their age, either wandered randomly about, cheeping loudly, or sat quietly in the center. During the 3 minutes when the sound-signal was being introduced their behavior was carefully recorded, and, at a later date, their responses scored according to the following scale:

X: moved directly to the sound source within two minutes and remained there until the tape's end, or approached to within 12 inches of the sound source and emitted soft pleasure-notes. In both cases, responses were scored **X** only if the duckling did not behave similarly towards other shoe-boxes.

a: ambivalent behavior, the duckling alternately approached and left the sound source, or an approach was made only after 2 minutes, or it responded by changing the nature of its calls from distress to pleasure-notes, without approaching.

O: continued behaving as before the introduction of the sound-signal.

-: showed fright reaction; the duckling moved rapidly to the opposite side of the apparatus and cowered quietly there, or ran about excitedly, cheeping very loudly, or suddenly ceased cheeping and "froze."

This schema was established on the basis of observations of normally reared wild ducklings, which responded in one of these ways to their own parents or to other sounds with which they were confronted.

It is clear that by the time a bird has been subjected to the first trial, a host of learning processes could have occurred which might easily have obscured the significance of subsequent responses. The lack of patent reenforcement following an **X** response, the particular sequence of the sounds, and the physical state of the duckling all could easily influence the responses to subsequent sounds. To assess the importance of these factors, replications of many tests were made at intervals of 12, 24 and 48 hours, the same birds being subjected to these repeated tests. As most birds showed fair consistency in their responses within the span of at least 2 test series, which could be up to 24 hours apart, it was felt that no major behavioral changes were occurring during the course of any one series. As an additional check, however, the sequence in which the sounds were presented was altered from one series to the next, and only the first series to which any one

duck was subjected was included in the data summaries and analyses. Finally, in order to compensate for other factors, such as fatigue, habituation, and reenforcement, the following precautions were observed:

1. Responses were scored only so long as the bird remained active. Thus all trials within any one series were discounted after the bird made no further movements; *e.g.* in a sequence to which responses were, in order, **X, 0, a, 0, 0, 0,** the last three trials were counted only if the bird had been active during the final trial. Experience had shown that once a bird which had been active lapsed into complete quietude, it would seldom resume activity in less than half an hour, whatever the stimuli. Such birds were retested a short time later.
2. Birds that had been allowed to follow were not carried or otherwise handled except in boxes or when their feet dangled freely, a position not favored by any duckling and one not likely to reenforce their following.
3. Birds were transported from brooder to apparatus in small cartons, though a few were carried this short distance without being placed in containers, their feet dangling, as above.

A review of the individual protocols reveals some disparity in the treatment which different ducks received, there being no rigid standard interval or age at which they were tested, the number of trials per series occasionally varying, and even the intervals between trials being somewhat erratic and of varying length. All these differences in treatment were unavoidable because ducklings, like most animals, show individual differences in their behavior and physical condition. Within a single clutch one bird might be walking easily by 6 hours of age and another not until 14. Some birds emerged entirely from the shell within 8 hours after pipping, many required 12, some were still struggling with their shells when they had pipped 16 hours earlier.

The following were the sound-signals used: female mallard quacks, emitted when the bird was placed in a wire enclosure with her brood remaining outside; the loud whistle of a male woodduck usually given in alarm situations; calls emitted by a pair of Emperor geese leading their young away from a human intruder; calls of a pair of Canada geese under similar duress; a rapidly repeated "pip" sound; a sequence of "KOM, Kom, kom"; a slowly repeated disyllabic "hel-lo"; and a sequence of notes, regularly repeated, on the flute. Audiospectrographic recordings showing the essential differences between these sounds are given in Figures 2-9.

It should be noted that these signals can be divided into at least 2 principal categories: sounds consisting of discrete phrases within a narrow frequency range, *i.e.* little variation in frequency from one phrase to the next (kom, pip, hello, Emperor, Mallard) and those with phrases which are less discrete and show a more musical variation in frequency (Woodduck, flute).

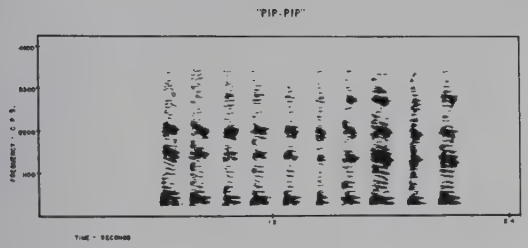
From the nature of the sounds used, it will be clear that what was being analyzed usually was not the manner in which ducklings learn to recognize their own species' calls but rather how they learn to recognize specific sounds which may be only vaguely similar to those of their normal experience. The difficulty of obtaining the particular sounds needed from all of the species used was too great to be overcome with the recording equipment available. The data, however, seem to justify the assumption that the learning process analyzed was identical to that which normally operates. The only qualification lies in the possibility that some of the species tested would have shown innate responses to certain other sounds had these been presented.

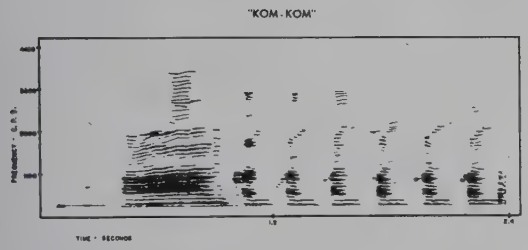
Data and Analyses

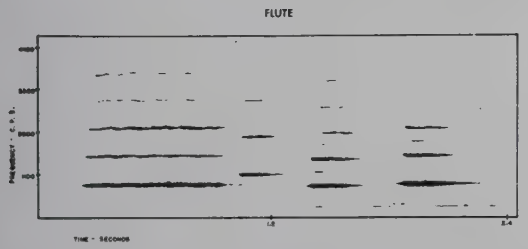
In the analyses that follow, ducks were divided into 2 major categories on a predetermined basis. Thus, it was assumed that hole nesting species, in which the duckling's first response must necessarily be to auditory rather than visual stimuli, would show learning patterns different from those of surface nesting species. The various surface nesting species used could not be considered separately because of a paucity of material during the initial phases of this study. Thus, Tables I and II represent data for mixed-species groups. The proportion of any one species is roughly similar in the different experimental groups, though more individuals of some species, *e.g.* mallards, were used than of others, *e.g.* Chiloe widgeons.

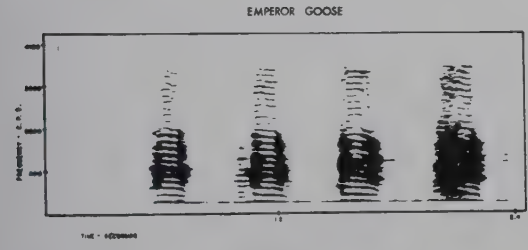
Table I. Surface nesting ducks and geese. A. Responses of isolates to sound signals

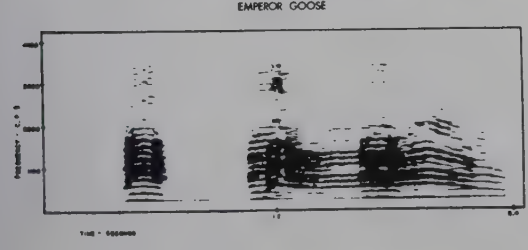
Signal	Proportion of tested birds giving a + response	Proportion of tested birds giving a + response exclusively to one particular sound
"Pip-Pip"	8/12	1/12
"Hello"	4/12	1/12
"Kom-Kom"	6/12	1/12
Flute	3/12	0/12
Emperor Goose	6/12	0/12
Mallard Duck	3/12	0/12
Wood-Duck	3/12	0/12

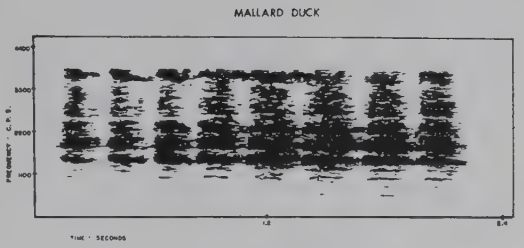


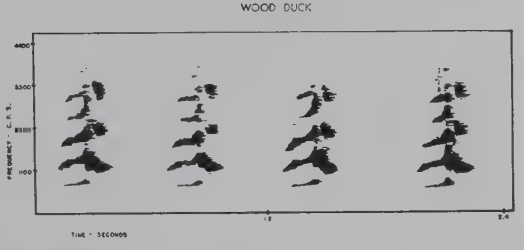












FIGS. 2-9. Audiospectrographic recordings of the sound-signals. The abcissae represent time in seconds, the ordinates frequency in cycles per second. Amplitude is indicated by the intensity of shading.

TABLE II. Surface nesting ducks and geese. B & C. Responses of birds exposed to sound and to sound with experimenter. "Relevant Signal" refers to the sound to which the ducklings were initially exposed

Relevant Signal	*B. Sound Only* Proportion of birds tested giving a + response exclusively to the relevant signal	*C. Sound with Experimenter* Proportion of birds tested giving a + response exclusively to the relevant signal
"Pip-Pip"	2/ 8	6/ 9
"Hello"	0/ 8	5/ 8
"Kom-Kom"	1/ 8	5/ 8
Totals	3/24	16/25
95% confidence intervals	.33 to .25	.43 to .83

The domestic Muscovy was considered separately since this bird, though a member of a perching, hole nesting tribe, utilizes an immense variety of nesting sites in its domestic situation and is also strikingly nonvocal, especially when compared with its closest relatives, the woodduck and mandarin duck (*Aix galericulata*) (Cotter 1957).

Results with Surface Nesting Ducks and Geese

Results of trials with 61 ducklings of surface nesting birds are given in Tables I and II. As controls establishing the normal behavior pattern, 2 clutches of wild mallard ducklings were trapped between 24 and 48 hours after they had hatched and their responses to different sound signals noted. In addition, 3 geese which had been hatched

under Bantam hens were tested. In every case an **X** response was given exclusively to the sound emitted by the bird which had hatched the young, in the first instance the mallard's call, in the second the Bantam's. These results corroborated observations in the field which had indicated that even when their mother swam out of sight behind rocks or bushes, as soon as she called, her young would speed directly to her, even when other species were calling close by.

The responses of the Isolates (Table I) show clearly that between the ages at which these birds were tested no exclusive preference for any one of the 7 sound-signals was demonstrated. It is possible, of course, that a preference does exist for some other signal that was not tested. However, this is rendered highly improbable by two facts: In the first place, half or more of the birds responded to all of the sound-signals characterized by short, discrete phrases. This is in accord with the findings of Fabricius (1951a), whose ducklings responded to rhythmic sounds, and with the suggestion of Marler (1955) that the source of this type of signal is easily located in space. The signals which can be characterized by the presence of several different frequencies during each phrase, or by the absence of discrete phrases (woodduck, flute, hello, mallard) were less popular. Curiously, as many birds showed a fear response to these latter signals (excepting hello) as showed a preference for them. The numbers involved, however, are too small to be statistically significant.

The second fact speaking against an innate preference is to be found in the results of the tests of birds which had been exposed to sound-signals while following (Table II, C). Whereas those birds which were exposed to sound only (II, B) showed no greater preference for the relevant signal than did the isolates, those which had been permitted to follow while hearing a sound subsequently showed a significant preference for that sound. Another group of birds was exposed to a sound-signal 12 hours before hatching, but this treatment produced no exclusive preference for the relevant signal. Even the "hello" signal, which was less favored by the isolates, was readily learned by the birds of the Sound with Experimenter group. It is clear, therefore, that the specificity to a particular sound which is shown by these ducklings in nature is initially the consequence of a form of learning in which the necessary unconditioned stimulus is a slowly receding visual stimulus, with which an auditory stimulus may then be associated. Reenforcement of appropriate responses to these auditory stimuli (in such forms as brooding and feeding) need not occur until a later time. This delay of reenforcement until after learning has occurred, though difficult to account for on older theories of learning, has much in common with latent learning, as Thorpe (1956) and others have pointed out. Whatever its basis, its adaptive significance is that it assures rapid and complete learning of an appropriate response at an early age.

Results with Woodducks

Results of experiments with 60 young woodducks are given in Tables III and IV.

TABLE III. Wood duck (*Aix sponsa*). A. Responses of Isolates to Sound Signals

Signal	Proportion of birds tested giving a + response	Proportion of birds tested giving a + response exclusively to one particular sound
"Pip-Pip"	2/12	0/12
"Hello"	0/12	0/12
"Kom-Kom"	1/12	0/12
Flute	3/12	0/12
Emperor Goose	0/12	0/12
Mallard Duck	0/12	0/12
Wood-Duck	1/12	1/12

TABLE IV. Wood duck (*Aix sponsa*). B. & C. Responses of birds exposed to sound and to sound with experimenter. "Relevant Signal" refers to the sound to which the ducklings were initally exposed

	B. Sound Only	*C. Sound with Experimenter*
Relevant Signal	Proportion of birds tested giving a + response exclusively to the relevant signal	Proportion of birds tested giving a + response exclusively to the relevant signal
"Pip-Pip"	6/ 8	1/ 8
"Hello"	1/ 8	0/ 8
"Kom-Kom"	6/ 8	0/ 8
Totals	13/24	1/24
95% confidence intervals	.32 to .75	0 to .23

In young woodducks, as in the species included among the surface nesters, there exists an ability to distinguish sound-signals. Field observations have shown that ducklings of not more than 2 or 3 days of age will promptly congregate at the site from which their mother is calling, even when she is not visible. R. Morrill (personal communication) has filmed the emergence of young woodducks from their nests and states that this exodus occurs in response to the calls of the female when she is off the nest and invisible to her young. In this respect hole-nesters are distinguished from the surface-nesters. The latter, when they first

respond to parental calls, have available to them visual stimuli as well. This does not mean that visual stimuli may not play a role for hole-nesters in the departure from the nest. Indeed, about one-third of the woodducks tested spent part of the time in the testing apparatus jumping up against the light bulb which hung over them, something none of the other ducklings did. This would suggest the existence of a releasor constituted by a light object in a darker field, which is the pattern presented by the nest entrance. The direct orientation to the female upon emergence, however, seems clearly to be an auditory process.

The responses of the Isolates (Table III) differ remarkably from the responses of the corresponding group among surface-nesters. Instead of showing a generalized tendency to respond to any rhythmic signal, the woodducks showed no significant tendency to respond to any of the signals. In a total of 84 trials, woodducks gave only 7 responses to any signal, compared to 33 responses in 84 trials in the case of the surface-nesters. The confidence limits of these two proportions at the 95% level do not overlap. When the birds are exposed to a particular sound, however (Table IV, B), a high proportion of the birds develop a specific preference for that sound. This proportion is significantly higher than either the proportion representing the number of surface-nesters from the corresponding group developing a particular preference (Table II, B) or that representing the number of Isolate woodducks with a particular preference (Table III). Clearly, auditory imprinting can occur in this species and, as will be shown, is probably the process operative in nature.

An examination of the values expressing the responses to the different signals used will reveal that "hello" was learned one one-sixth as often as either "pip" or "kom." While the numbers involved are too small to allow a definite statement, it might be the case that woodducks can learn some patterns of sound more readily than others. This is also suggested by the fact that of the 7 responses of the Isolates (Table III), 5 are clustered about 2 signals, and 3 signals were not responded to at all. Of the surface-nesters' responses (Table I), 14 of the Isolates' 33 responses were clustered about 2 signals. However, these 2 proportions do not differ significantly. At best, all that can be said is that the woodducks may have preferences for a signal other than those tested and that the possibility of their learning some sounds more readily than others is not precluded.

Allowing the young birds to follow the experimenter to the accompaniment of a particular sound did not increase the number of responses given to that sound. The values given in Table IV, C do not differ significantly from the responses of the Isolates shown in Table II. The birds from this Sound with Experimenter group, however, behaved quite differently from their homologues among the surface-nesters. Of the latter (Table V), 23 out of 24 followed me readily and well.

TABLE V. Number of ducklings from Group C which followed when given opportunity

Species	Number following/ Total tested	Confidence intervals at 95%
Surface nesters	23/24	.78 to .99
Wood-Ducks	14/24	.37 to .78
Muscovies	8/19	.18 to .65

When I stopped moving and crouched, continuing to call, they invariably clustered about my feet. Of the woodducks, only 14 out of 24 birds followed at all. The confidence intervals for the two proportions at the 95% level are .37 to .78 and .78 to .99. Thus the differences are just significant. When I stopped moving they would come as close as 2 feet, but would then either circle me nervously or else flee. Two explanations are possible. The developmental chronology may differ so that the following-response is inhibited by the fear response by the time motor coordination is achieved. Alternatively, the following-response may be learned in a fashion the reverse of that in which a young mallard learns a sound-signal, *i.e.* an imprinted sound may serve as a stimulus which is then associated with a visual conditioned stimulus.

The young of all the surface-nesting species tested were usually able to walk and follow readily as soon as dry, no later than 8 hours post-emergence, usually earlier. Uniformly, however, the woodducks showed a rate of motor development which was retarded when compared with these other birds. None was able to walk before 12 hours, and many proved too weak to stand until 18 hours. In mallards, the following-response begins to wane by 20 hours, and can rarely be elicited much after 24. It is conceivable that the fear response, which is presumed to inhibit following, may thus appear in woodducks before full motor coordination is achieved. In such instances, visual imprinting will not occur. The fact that more than half of the birds which could be made to follow did show a clear ambivalence towards the experimenter would strongly suggest this. The alternative explanation cannot be wholly discarded, however, for it was found that several woodducklings which had been imprinted to a

sound-signal alone would follow and approach closely as long as I was emitting the particular sound to which they had been imprinted. These birds were about 30 hours old, and thus well past the maximum age for the elicitation of the following-response in unimprinted birds. Unfortunately, the number of birds tested in this way was too small for statistical analysis.

In summary, the absence of unlearned preferences for any of the signals used, the general reluctance to follow, and the development of preferences for at least 2 different sounds as a result of early exposure to them, suggests that the young of this species learns its particular call through a process of auditory imprinting.

Results with Domestic Muscovies

From Tables VI and VII it will be seen that this breed did not respond to any of the signals used when raised under the conditions of isolation described previously (Table VI), and could not be trained to make any responses (Table VII).

TABLE VI. Domestic muscovy (*Cairina moschata*). A. Responses of isolates to sound singnals

Signal	Proportion of birds tested giving a + response	Proportion of birds tested giving a + response exclusively to one particular sound
"Pip-Pip"	1/12	1/12
"Hello"	0/10	0/10
"Kom-Kom"	0/12	0/12
Flute	2/12	0/12
Emperor Goose	1/10	1/10
Mallard Duck	0/12	0/12
Wood-Duck	3/12	1/12

TABLE VII. Domestic muscovy (*Cairina moschata*). B. & C. Responses of birds exposed to sound and to sound with experimenter. "Relevant Signal" refers to the sound to which the ducklings were initially exposed

Relevant Signal	*B. Sound Only* Proportion of birds tested giving a + response exclusively to the relevant signal	*C. Sound with Experimenter* Proportion of birds tested giving a + response exclusively to the relevant signal
"Pip-Pip"	0/ 4	0/ 6
"Hello"	0/ 7	0/ 6
"Kom-Kom"	0/ 7	1/ 7
Totals	0/18	1/19
95% confidence limits	0 to .18	0 to .18

In addition, those birds which were allowed to follow, proved more difficult to imprint visually than was the case for the other species. These results are given in Table V. It seems unlikely, *a priori,* that this is a condition obtaining in the wild state. Information on this point, however, is remarkably scant and it is a matter of great regret that wild birds were not available. Heinroth and Heinroth (1928) report having raised some young which were derived from one wild and one wild-domestic hybrid parent. These birds apparently behaved in a manner similar to that of the domestic birds. All else that can be remarked is that on the basis of serologic evidence the muscovy has its closest ally in the tribe Cairinini with the hole-nesting, highly vocal wood and mandarin ducks (Cotter 1957).

It would appear likely that the disappearance of the vocal characteristic and lack of nest site specificity are concommitants of domestication. This breed is devoid of any distinct call, the male being reduced to a low grunt and the female a hiss. It should also be added, in regard to the muscovy's nonvocal attributes, that it has retained a well developed syrinx and seems anatomically capable of producing as large a variety and as high a volum of sound as any other duck (Heinroth and Heinroth, 1928).

The effects of domestication on such traits as the ability to be imprinted cannot be considered here. Suffice it to say that in a barnyard situation, where imprinting onto a biologically inappropriate object can occur with much greater facility than in the wild, one would expect selection against the ability to be imprinted. Similarly, with the loss of voice—the muscovy's "quackless" nature being one of its selling points—the ability to learn sound-signals easily and rapidly would also be expected to decline.

Whether or not the wild races behave similarly, it is clear that the domestic muscovey departs radically from the pattern common to the other ducks tested, lacking as it does the ability to learn auditory signals rapidly. The possibility of an unlearned and highly specific preference for a single sound-signal remains, of course, though this breed's silent nature renders this highly unlikely.

Social Facilitation

One of the outstanding differences between the laboratory hatched stock and birds observed in the wild lies in the greater variability in the behavior of laboratory reared individuals. In a normally reared clutch all birds tend to act similarly and synchronously, with the consequence that the clutch behaves as a unit. In the laboratory, on the other hand, one might randomly choose 8 birds and find only a fraction acting identically under similar conditions when tested individually. When

allowed to function as a group, however, these ducklings too interact in a fashion that minimizes individual differences in response tendencies.

This social interaction was demonstrated by the following experiments: groups of ducklings were raised in brooders isolated from the sounds used in the previous experiments until 24 to 72 hours of age. These groups varied in size from 6 to 18 ducklings of several species. From one to 13 of these ducklings at a time were placed in the apparatus (Figure 1) together with from one to 3 ducklings which had been imprinted onto the experimenter and thereby trained to respond to a particular sound-signal. These "leaders," as they may be called, were reared together, though kept separate from the untrained "followers" until the time of the experiments. In only one case was a leader reared with the followers. The age composition of the groups tested—followers plus leaders—was randomized, so that the leaders were sometimes the oldest, sometimes the youngest, sometimes the middle-aged of the group. Similarly, sizes were randomized, some leaders being the minute Bluewing Teal, others the much larger Redheads of the intermediate Scaup (*Aythya affinis*).

A simple protocol will indicate the usual sequence followed during the course of a series of tests:

Ducklings in apparatus (listed by code name)[3]	entire groups' response to signal
1	O
1, W	X
1	O
1, W	X
1, 2, W	X
2	O
1, 2, W	X
3	O
3, 1	O
3, 1, 2	O
3, 1, 2, W	X

No group of ducklings was used for more than 3 series of tests, in order to avoid complicating effects such as conditioning due to handling. Altogether 7 different groups of followers and leaders were used, totalling 120 ducklings. The results are given in tabular form (Table VIII).

From the data it will be seen that with no more than 3, or occasionally 4, untrained followers to each leader, the latter can determine the behavior of the entire group, causing it to act as a unit. It is an effect which, however, seems to be purely mechanical. The rearing techniques precluded the formation of functional dominance hierarchies which, as a matter of fact, have never been observed in ducklings of these ages and species (*cf.* W. Smith 1957, and Weidmann 1956). The response of the group appeared to be to directed movement of any kind on the part of any of its members. When the leader was the only member moving, it was he that was followed. With more ducks in the group, the probability of some duckling other than the leader moving elsewhere increased, and with these larger groups the responses became less consistent. Increasing the number of leaders, in turn, increased the probability of its being one of the leaders that was followed. A sample protocol from a trial in which 5 followers were tested with 1 leader (W) will illustrate the ducklings' behavior under conditions when the ratio of leader to follower was such as not to lead to a uniform response:

"group immediately went to sound source, led by W, but left after several seconds, followed by W, and wandered randomly. W returned to sound source after a few seconds more, was followed there by the others which, after several seconds, wandered off again, followed by W (O)"

Again, here is a sample from a trial involving 9 followers and 3 leaders, one of which, B, was

TABLE VIII. Social facilitation tests. Proportion of trials giving + results

Total size of group	Responses with 1 leader	Responses with 2 leaders	Responses with 3 leaders
2	4/4		
3	6/6		
4	5/6		
5	2/8		
6	0/2	5/5	
7	0/3	5/5	
8	0/1	3/5	
9	0/1	1/3	
10	0/1	2/3	
11		3/3	3/5
12		1/3	4/5
13		1/3	3/5
14			1/5
15			1/5
16			1/5

	RESPONSES WITH LEADER	
	Follower ratio 1:3.3 or more	Follower ratio 1:4 or less
1 leader	14/15	2/15
2 leaders	13/15	8/15
3 leaders	10/15	3/15
Totals	37/45	13/45
95% confidence intervals	.62 to .92	.17 to .45

[3] Follower-ducks were given numbers, leader-ducks letters. Thus, in the above series, W is the only leader.

particularly steadfast in his responses to the sound-signal:

> B cheeps very loudly, moves towards sound source, halting halfway between it and group, which sits near center, preening, pecking at ground. After 15 seconds, B returns to group, still cheeping loudly, turns, goes back towards sound source, followed by group which sits by entrance (X)

Under some circumstances, the design of the apparatus made responses to a sound-signal unfavorable. Thus, with more than 10 ducklings in the apparatus, it would sometimes happen that the leader would be trapped against the sides of the apparatus, or in one of the shoe-boxes, by the densely aggregated followers. Following a trial when this occurred, the ducklings were replaced in the center of the apparatus, or caused to disaggregate by tapping the side of the apparatus before continuing the series.

This type of pacemaker effect has been termed social facilitation (Thorpe 1951), and its functional significance should not be underrated. It assures that all members of a clutch will respond properly even when some members have not themselves learned the proper responses. This is of particular significance with respect to the ability of precocial birds to be imprinted. As the critical period is lengthened, or as the bird's susceptibility to becoming imprinted increases the possibility of imprinting onto biologically inappropriate objects also increases. On the other hand, too short a critical period or too insensitive a condition would be equally hazardous. In the compromise which selection seems to have reached, only a certain proportion of the birds which were tested in the laboratory proved imprintable under the conditions of the experiment. But when placed together, groups of birds nonetheless acted as if all members had been similarly imprinted. The underlying genetical problems which this points to are of considerable interest for it is also possible that the differences in response tendency represent an instance of balanced polymorphism on a behavioral level. The learning capacities of ducklings are limited, so it might be of advantage for each duckling to learn a different response, provided a leadership principle such as that described were operative.

Conclusions

The unorganized and sketchy state of our knowledge of the inheritance of song and other vocalizations in the class Aves is still such as to require a great deal more in the way of comparative studies. Yet the problem is of great enough interest to justify some efforts at speculation, while a certain limited amount of corroboratory evidence is at hand. The model proposed here rests on the assumption that in precocial birds species-specific behavior must be established either prior to hatching or very rapidly thereafter. The exceptions are those cases where an extended relationship between young and parents continues after hatching, as in most of the Anatidae. In these instances there must exist other mechanisms that can operate shortly after emergence of the young and insure against separation and dispersal. As indicated, some of these mechanisms are closely allied with those involved in the learning of particular auditory responses. In altricial species, on the other hand, it is assumed that physical factors operate to insure an association of young with parents, allowing responses to specific vocalizations, and the vocalizations themselves, to be learned in a more gradual fashion. Again, the exceptions might be expected in those species for which the *Umwelt* is especially stable and where it might thus be advantageous to relegate this category of behavior to neural circuits established before hatching.

As the ancestral birds were presumably precocial, the evolutionary sequence may have been from a condition where auditory behavior and responses were established before hatching to one where they were determined by rapid learning directly after hatching. Thereafter, as the class radiated and evolved, some groups delayed the learning process, pushing it later into ontogeny, while others pushed it back again to a point before emergence from the egg. As indicated by the differences among the species of water-fowl tested, minor changes are superimposed on these processes by the particular environments affecting the species. The nature of these latter differences and the reasons for them are easy to see. It is expected that studies of other hole-nesters, *e.g. Bucephala clangula* or *Mergus* sp., will confirm the relation between the hole-nesting habit and the type of auditory imprinting of which the wood-ducks proved capable.

The ability of a relatively small proportion of ducklings in a brood to act as pacemakers, synchronizing the activities of the brood as a whole, will not surprise those who have spent any number of hours observing wild ducks. It is of interest, however, that this effect is manifest even when the leaders have been with the group but 30 to 60 seconds before the tests. This tends to emphasize the mechanical nature of the effect, and the irrelevance of dominance relations.

Summary

The surface-nesting species of waterfowl that were examined were shown to learn the appro-

priate sound-signal involved in the maintenance of the brood-parent relationship as a consequence of visual imprinting. No unlearned preferences for any particular auditory signal seemed to exist, nor could auditory imprinting occur in the absence of visual stimulation. This situation was reversed in the woodduck. In this hole-nesting species, exposure to a sound-signal alone could produce a subsequent preference for that sound, demonstrating auditory imprinting. The imprinted responses was not reenforced or altered in any way by following or by a visual stimulus. This fact is explained by the nesting habits of woodducks which require that the young ducklings' first response to their mother is based on auditory stimuli. In surface-nesting birds, visual cues can play a larger role from the start and thus assume paramount importance.

The quackless muscovy was shown to be incapable of auditory learning under the conditions of the experiment, and this remarkable failure in a species related to woodducks is presumed to be a consequence of domestication.

The effects of social facilitation were analyzed, and evidence is presented accounting for the uniformity of behavior shown by a brood, the members of which, when tested individually, showed much variability in their response tendencies. A trained duckling can apparently stimulate 3 to 4 untrained ones to act in similar fashion. This effect seems to be purely mechanical. Pre-existing social relations are unnecessary and dominance relations play no role. The directed movement of one duckling acts as a stimulus for others. Such a leadership phenomenon suggests that a balanced polymorphism on a behavioral level might prove highly adaptive.

A model for the evolution of auditory learning mechanisms is proposed which assumes that in precocial birds species-specific behavior must be established either prior to hatching or else very rapidly thereafter. Exceptions are to be found in groups with extended familial relations. In these groups other mechanisms, operative shortly after hatching, ensure against separation and dispersal. In altricial species, on the other hand, it is assumed that physical factors operate to insure an association of young with parents, allowing responses to be learned in a more gradual fashion. The exceptions here are to be found in species with an especially stable *Umwelt* for which it might be advantageous to relegate this category of behavior to neural circuits established before hatching. Throughout, it is assumed that there is no qualitative difference between behavior established prior to the animal's birth and behavior that is determined during specific periods shortly after birth or established gradually during the animal's life. The amount of any animal's behavior that lies within any of these categories is determined by the stability of its environment, the degree of motor precocity, and the amount of neural material available.

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This study is dedicated to Thomas Klopfer, whose untimely death has made both Psychology and mankind the poorer.

References

Collias, N. and E. Collias. 1956. Some mechanisms of family integration in ducks. Auk **73**: 378-400.

Collias, N. and M. Joos. 1953. Spectrographic analysis of sound signals of the domestic fowl. Behaviour **5**: 175-187.

Conradi, E. 1905. Song and call notes of English sparrows when reared by canaries. Am. Jour. Psych. **16**: 190-198.

Cotter, W. 1957. A serological analysis of some Anatid classifications. Wilson Bull. **69**: 291-300.

Ewer, R. F. 1956. Imprinting in animal behaviour. Nature **177**: 227-228.

Fabricius, E. 1951a. Zur Ethologie Junger Anatiden. Acta Zoologica Fennica **68**: 1-175.

———. 1951b. Some Experiments in Imprinting Ducklings. Proc. X International Ornithological Congress: 3755-379.

Fankhauser, G. 1955. Effect of size and number of brain cells on learning in the larvae of *Triturus v.* Science **122**: 692.

Forbush, E. H. 1925. Birds of Mass. and other New England States, Vol. **1**, Mass. Dept. Ag.

Frith, J. 1956. Breeding habits in the family Megapodidae. Ibis **98**: 620-640.

Frings, H. 1955. Recorded calls of herring gulls as repellants and attractants. Science **121**: 340-341.

———, **et al.** 1955. Auditory and visual mechanisms in food finding behaviour of Herring Gulls. Wilson Bull. **67**: 155-170.

Heinroth, O. 1910. Ethology und Psychology der Anatiden. Verh. d. v. Intern. Ornithological Kongress: 590-702.

——— **and M. Heinroth.** 1928. Die Voegel Mitteleuropas, Bd. I-III. Berlin.

Hess, E. H. 1955. Progress Report, Public Health Service Grant #M. 776 (not published).

Hinde, R. A. et al. 1956. The following responses of young coots and moorhens. Behaviour **9**: 214-242.

Holmgren, N. 1955. Studies on the phylogeny of birds. Acta Zoologica **36**: 243-328.

Howard, H. 1950. Fossil evidence of avian evolution. Ibis **92**: 1-21.

———. 1947. Preliminary survey of trends in avian evolution from the pleistocene to the Present. Condor **49**: 10-13.

Jaynes, J. 1956. Imprinting: the interaction of learned and innate behaviour. Jour. Comp. Uhysiol. and Psych. **49**: 201-206.

Kendeigh, S. C. 1952. Parental care and its evolution in birds. Illinois Biological Monograph **22** (1-3).

Lorenz, K. 1941. Vergleichende Bewegungstudien an Anatiden. Journal für Ornithologie **89**: 194-294.

———. 1935. Der Kumpan im Unwelt des Voegels. Journal für Ornithologie **83**: 137-213.

Marler, P. 1956a. Ueber die Eigenschaften einiger Tierliche Rufe. Journal für Ornithologie **97**: 220-227.

———. 1956b. The voice of the chaffinch and its function as language. Ibis **98**: 231-261.

———. 1955. Characteristics of some animal calls. Nature **176**: 6-8.

———. 1952. Variations in the song of the chaffinch. Ibis **94**: 458-472.

Messmer, E. and J. Messmer. 1956. Development of calls, song and other behaviour in the blackbird. Zeit. für Tierpsychologie **13**: 341-441.

Metfessel, M. 1935. Roller canary song produced without learning from external sources. Science **81**: 470.

Nice, M. 1953. Some experiences in imprinting ducklings. Condor **55**: 33-37.

Petrunkevitch, A. 1926. Value of instinct as a taxonomic guide in spiders. Biol. Bull. **50**: 427-432.

Poulsen, H. 1951. Inheritance and learning in the song of the chaffinch. Behaviour **3**: 216-228.

Pringle, J. W. S. 1950. On the parallel between learning and evolution. Behaviour **3**: 174-215.

Ramsay, A. O. and E. H. Hess. 1954. Laboratory approach to the study of imprinting. Wilson Bull. **66**: 196-206.

Sauer, F. 1955. Entwicklung und Regression Angeborenen Verhaltens bei der Dorngrassmuecke. Proc. XI Intern. Ornithological Congress: 218-226.

Scott, J. P. and M. Marston. 1950. Critical periods affecting the development of normal and maladjustive social behaviour in puppies. Jour. Genetic Psychol. **77**: 25-66.

Simms, E. 1955. Conversational calls of birds as revealed by new methods of field recording. Acta XI Cong. Internat. Ornithology: 623-626.

Smith, W. 1957. Social learning in domestic chicks. Behaviour **11**: 40-55.

Spalding, D. A. Reprinted 1954. Instinct. Brit. Jour. Animal Behav. **2**: 2-11.

Spurway, H. 1954. The causes of domestication. Jour. Genetics **53**: 325-62.

Stadler, H. 1926. Dievogelstimforschung als Wissenschaft. Verh. VI Internat. Ornithological Kongress: 338.

Stevens, D. M. 1955. Transference of imprinting in a wild gosling. Brit. Jour. Animal Behav. **3**: 14-17.

Thorpe, W. H. 1956. Learning and Instinct in animals. Methuen: London.

———. 1951. Definitions of terms used in animal behaviour studies. Bull. An. Behav. **9**: 34-41.

Vernon, J. H. and J. Butschi. 1957. Effect of tetraploidy on learning and retention in salamanders. Science **125**: 1033-4.

Weidmann, U. 1957. Verhaltensstudien an der Stockente Zeit. für Tierpsychologie **13**: 208-271.

THE EFFECTS OF FIRE ON A POPULATION OF SMALL RODENTS

SHERBURNE F. COOK, JR.
Museum of Vertebrate Zoology, Berkeley, California

INTRODUCTION

The influence of fire upon the succession of plants in western North America has been the subject of much study. Much less attention has been paid, however, to the corresponding succession of animals that is likely to accompany the habitat alterations occurring in a seral progression. The aim of this study is to measure the recovery rate of small rodent populations after a fire. It was not possible to attempt a detailed vegetative analysis, and discussion of floristic changes will be limited to those general features that might have a direct influence upon rodent populations.

The study was carried out in Tilden Regional Park, one mile east of Berkeley, California, where, on October 21, 1953, a wild-fire burned 600 acres along the east side of this 2500 acre park. The fire was started by a power line, blown down by a dry, warm, north wind that was measured at over 70 mph in gusts. As a result of the ex-

treme wind velocity and the dryness of the landscape, the fire swept across the area very rapidly. The basic plan of the study was periodically to sample the mammal populations on the burn and on adjoining unburned ground by snap-trapping. Any differences in numbers of animals caught could be interpreted as a function of the burn. Trapping was started 3 weeks after the fire (on Nov. 5, 1953), and was carried on at regular intervals until April of 1956. The data obtained are the result of 11,880 trap nights.

I wish to thank Dr. A. S. Leopold for his help and advice throughout this study, as well as Drs. O. P. Pearson, H. H. Biswell, and R. D. Taber, who offered valuable suggestions on the manuscript. Further, I am indebted to Dr. Robert S. Hoffmann for valuable supplementary data furnished me from a population study in an adjacent area.

Description of Area

The total area burned in this fire was a strip approximately 2 miles long and half a mile wide along a west facing slope in the hills east of Berkeley. The burned area represented a small portion of an extensive region of similar habitat and was confined on all sides by fire trails and roads. The territory covered consisted mainly of mature grassland with about 200 acres of scattered brush and a few small groves of eucalyptus and young planted *Pinus radiata.* Two habitat types were considered in this study—grassland and brush. Both areas were burned completely and reduced to ash, except for a few charred snags and stubs of brush.

Grassland Habitat

The grass area was a complex of many species of plants with no one species dominating anywhere except very locally. It had been ungrazed and undisturbed for about 20 years. When the fire went through, it was stopped on the north by a fire road which separated 2 portions of a large continuous grassland. This made a sharp dividing line between burned and unburned areas and it seemed safe to assume that the original floristic composition had been the same on both sides of the fire road. This vegetation included a large variety of grasses, such as *Avena fatua, A. barbata, Bromus* spp., and *Lolium multiflorum,* together with such herbs as *Conium maculatum, Brassica* spp., *Galium asperrimum, Vicia americana, Cirsium* sp., *Chlorogalum pomeridianum,* and *Geranium* sp.

After the fire, ground cover on the burned grass area was almost completely lacking except for an occasional rock. Grass seeds were abundant and seemed relatively unaffected by the fire except for popped seed coats. With the first rain of winter, on November 13, 1953, germination took place rapidly and within a week the area was a mat of green grass and small herbs. Throughout the spring the area was dominated by *Avena barbata,* with *Anthemis cotula* and *Vicia americana* growing in large patches. By summer there were a few scattered thistles, tar weed, and mustard.

The second year's growth on the burned grass area showed slightly greater variety but it was still dominated by *Avena.* Also, much mulch or litter had accumlated from the previous year's annual grass crop and cover seemed quite adequate to support grass-dwelling rodents.

By the third spring after the fire (April, 1956), differences between the burned and unburned grass areas were still apparent. The burned side still was dominated by annual grasses—mostly *Avena*—and large patches of *Vicia americana.* The *Anthemis* had been largely replaced by *Geranium* sp., *Vicia* and other small herbs common in the complex of many dominants remaining on the unburned side.

Brush Habitat

The other habitat type affected by the fire was brush. No sharp dividing line existed here between burned and unburned areas. It was only through previous familiarity with the terrain that it was possible to select a control area that was similar to the burned brush prior to the fire.

The burned brush area selected for trapping had consisted of *Baccharis pilularis, Rhus diversiloba,* and *Artemisia californica* interspersed with grassy patches and a scattering of *Conium* in the more moist parts. The control area selected closely resembled the burned area, as reconstructed, insofar as exposure, ground moisture, and floristics are concerned.

Immediately following the fire no green growth could be seen. The fire left only the ash-covered larger branches of the *Baccharis* and *Rhus* and mere stumps of the *Artemesia.* Ground cover was nonexistent except for a few large rocks and rock outcrops.

With the first winter rains came a mat of herbs and grasses. By late spring *Avena barbata* once again dominated all the higher ground but was far less dense although taller in the area previously dominated by *Artemisia* than in the areas of previous grass. There was less *Anthemis* and *Vicia* than on the grassland but more thistles and *Diplacus aurantiacus* around rock outcrops. The

Artemisia began to sprout around the base of the old snags in the spring and continued to grow sparsely. A few seedlings were present. By the second winter the *Artemisia* was growing well but very sparsely, *i.e.* each plant contained a few tall shoots rather than the normal bush-like cluster.

Most of the *Baccharis* was not completely killed, for in the first spring after the fire new sprouts appeared out of the old burned branches and around the base of the plants. The root sprouts of the *Rhus* reappeared more slowly than those of the *Baccharis*.

By the end of the third year's growing season the *Artemisia,* although coming along, was still sparse and overshadowed by the *Avena*. *Diplacus aurantiacus* had increased significantly on the drier slopes, while the *Baccharis* had almost regained its status of before the fire.

Methods and Procedures

After suitable trapping areas had been selected, trap-lines were staked out according to one method prescribed by Calhoun (1948). These lines consisted of 20 stations, 25 feet apart, with 3 snap-traps set in the most likely spots (*e.g.* runways within 2½ feet of each stake. In this way 60 traps were set out and checked every morning for 3 mornings, making 180 traps nights per trapping period. Since only an indext of abundance rather than a total count was sought in comparing one line with another, live trapping was considered unnecessary. To avoid over-trapping in the burned grassland, two parallel lines 200 feet apart were staked out. Since the whole area was a continuous grassland it was felt that each line could be trapped on alternatie months thereby permitting monthly trapping while allowing 2 months for recovery of the mice. Therefore, the burned grassland was trapped every month, and the unburned grassland control was trapped only on alternate months even though 2 parallel lines were used as in the preceding case.

Because of limited area, only one line was staked out in the brush areas. The burned brush was trapped every other month and the control every 4 months.

Traps were baited with a mixture of rolled oats and peanut butter, mixed into a thick paste. Except, perhaps for *Reithrodontomys,* there was little of the correlation between bait acceptance and the availability or scarcity of natural foods that was found by Fitch (1954). Fitch, however, was apparently using live traps which are generally more dependent upon bait attraction than are snap traps which can be set across runways.

Trapping was carried out at prearranged dates regardless of weather or moonlight. These phenomena were found to have little effect upon the activity of the mice.

Results

Grassland Habitat

Figure 1 represents the total numbers of mice trapped in the grassland for each trapping period from November, 1953, until April, 1956. These mice include the species listed in Table I. Figures 2 and 3 show the fluctuations in numbers of the two dominant species in the areas—*Reithrodontomys megalotis* and *Microtus californicus.*

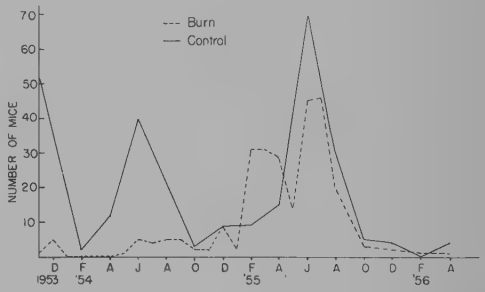


Fig. 1. Total catch for all species in the grassland.

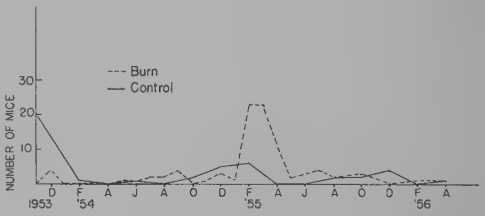


Fig. 2. *Reithrodontomys* fluctuations in the grassland.

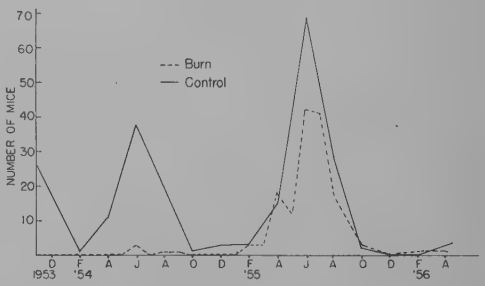


Fig. 3. *Microtus* fluctuations in the grassland.

In Figure 1 it can be noted that the mice in the unburned area exhibit presumably natural annual population fluctuations. The mice on the burned area, on the other hand, show an initial annihilation and a general low density in total numbers until the late winter of the second year when there was a sudden increase. This was caused by

TABLE I. Grassland

Trapline 1 Burn	1953		1954												1955												1956		
	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A
Microtus californicus								3		1	1					3	3	18	12	42	41	17		3				1		1
Reithrodontomys megalotis		4					1	1	2	2	4		1	3	1	23	23	11	2	3	4	2			1					
Sorex ornatus										1							5					1			1				
Mus musculus														1		3													
Peromyscus maniculatus	1	1						1	2	1		2	1	5	1	2					1								
Total	1	5	0	0	0	0	1	5	4	5	5	2	2	9	2	31	31	29	14	45	46	20		3		2		1		1
Trapline 1 Control																														
Microtus californicus	26			1		11		38		19		1		3		3		15		68		28		2						3
Reithrodontomys megalotis	20			1				1				2		5		6						2		2		4				1
Sorex ornatus	2					1				2										2				1						
Mus musculus																														
Peromyscus maniculatus	4							1						1																
Total	52			2		12		40		21		3		9		9		15		70		30		5		4		0		4

a sharp increase in the population of *Reithrodontomys* (Fig. 2) which quickly gave way to a large increase in *Microtus* later in the spring of the second year after the fire (Fig. 3).

Table I and Figure 3 show a stabilization of the *Microtus* population between the burned and unburned areas during the second year's growth while the population was at a low ebb.

As may be noted in Table I and Figure 2, *Reithrodontomys* began to invade the burned area in the early summer of the first year during the period of maximum seed production of the annual grasses. Likewise *Peromyscus maniculatus* started to invade the burned area at about the same time and remained at a rather constant and probably significantly higher density than on the unburned grass during this second year.

Reverting to *Reithrodontomys,* this usually common mouse profoundly decreased in numbers on the unburned area immediately following the first trapping and has as yet failed to recover. On the burned area the species paralleled in number the natural population until the late winter of the second year when it irrupted. However, instead of the numbers continuing upward, as one might exepct with the breeding season coming in March, they fell off in the early spring and have remained at a low ebb ever since. This transitory irruption of *Reithrodontomys* is set forth numerically in Table I and Figure 2.

Invasion of the burned area by *Mus* was noted in the winter of the second year. Although the numbers shown in Table I are small, they are supplemented by additional trapping conducted at this time that produced several *Mus* in another region of the burned area. The catch of *Mus,* as small as it is, shows a fairly obvious preference on the part of this mouse for a habitat such as that created by the fire. No *Mus* were taken on the unburned area during this study, nor were any caught by Dr. Robert Hoffmann after considerable trapping in an adjacent unburned grass area.

Brush Habitat

Mice of the burned brush habitat, after initial annihilation, exhibited a population increase that surpassed that of the control throughout the second year following the burn (Figure 4).

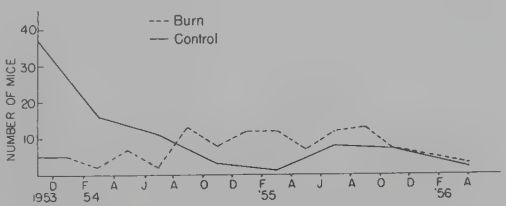


FIG. 4. Total catch for all species in the brush areas.

As far as species are concerned, brush areas are more or less dominated by 3 species of *Peromyscus: P. maniculatus, P. californicus,* and *P. truei. Microtus* and *Reithrodontomys* are present only in localized spots where grass and herbaceous growth dominate.

TABLE II. Brush

Trapline 2 Burn	1953		1954												1955												1956			
	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A
Microtus californicus							2		2						1		4		4		5		3							
Reithrodontomys megalotis			1								3		3		6		4		2		4		8		6					3
Perognathus californicus											5						1				2									
Peromyscus maniculatus	4		3		1		3				5		5		4		2				1		2		1					
Peromyscus californicus			1																											
Peromyscus truei	1				1		2																							
Sorex ornatus															1		1		1											
Total	5		5		2		7		2		13		8		12		12		7		12		13		7					3
Trapline 2 Control																														
Microtus californicus	5								3												3				4					1
Reithrodontomys megalotis	6				1																				1					
Perognathus californicus																					1									
Peromyscus maniculatus	22				10				4				1								3				2					1
Peromyscus californicus	4				3				3				1				1				1									
Peromyscus truei					2				1				1																	
Sorex ornatus																														
Total	37				16				11				3				1				8				7					2

In Table II it may be noted that on the burned brush area the *Reithrodontomys* increased as the grass took over on areas of previous brush, whereas the *Peromyscus maniculatus* remained relatively constant. Few *P. californicus* and *P. truei* were trapped in this area and these species disappeared after the first spring. It is presumed that those trapped in the early stages after the fire were individuals that had remained in the area in spite of the fire. The *Microtus* also increased slightly but did not approach the population levels of the grass areas. *Perognathus californicus* occurs in this area, although it is rather uncommon compared to other species. Results show, however, the appearance of these mice in the late summer of the first year on the burned brush area.

The unburned, or control brush area exhibited a greater sustained population decline than did any other area. All species here underwent a severe reduction until at a period late in this study only one *Peromyscus californicus* was taken in 180 trap nights. It is possible in this case that emigration from the burned area 100 yards away could account for a portion of the initial catch. However, mouse densities at this time were up in this region and the initial catch was not unusually high.

REPRODUCTION DATA

Data on reproductive condition were obtained through the kindness of Drs. Robert Hoffmann and Oliver P. Pearson who examined most mice caught for reproductive state and approximate age. Their findings revealed the following facts: *Reithrodontomys,* according to Dr. Pearson, do not breed until late March and on through the spring. Reproduction slows down in the summer and increases again in the early fall, ceasing in the late fall. The *Microtus* in this area are not so restricted to a breeding season and some may breed the year around. Generally speaking, however, *Microtus* show a breeding cycle similar to *Reithrodontomys* and other species, although the season starts earlier—usually in February. This was found to be the case in the late winter of the second year when the *Reithrodontomys* irrupted. All the female *Microtus* trapped during this period were found to be pregnant or lactating with no juveniles taken. No pregnant or lactating *Reithrodontomys* were taken until the

April trapping, in spite of the outbreak on the burned area 2 months previously.

Discussion

When this study was first contemplated it was thought that a fire would reduce the populations of small mammals either by killing them directly or by indirect means resulting from removal of food and cover. There was no evidence to suggest that surviving mice emigrated to adjacent unburned areas, and food in the form of seeds was virtually unaffected by the fire. That many of those mice with shallow burrow systems were killed by the fire directly is no doubt true; nevertheless, the actual cause of the initial annihilation is still in doubt.

After this initial extermination it would appear that recovery of small rodent populations was restricted on the burned areas during the first year chiefly by deficiencies in cover. Certainly food was abundant for seed eating mice by early spring of the first year when all the annual grasses were starting to go to seed, and succulents for the grass eaters were very abundant by January of the first year. Since the grass-dwelling mice, especially *Microtus,* build surface runways as a by-product of their activity, they apparently need at least one year's accumulation of mulch to afford cover.

During the second year's growth, conditions reached an optimum for *Reithrodontomys* in the grassland. The data furnished in Table I and Figure 2 are further substantiated by a March, 1955 trapping by Dr. Robert Hoffmann. His traplines were further from the burned area than the control lines used in this study. His results during this period show a catch of one *Reithrodontomys* during 180 trap nights, whereas the control lines of this study during the same period show 6 *Riethrodontomys* (for February) while the burn produced 23 animals on each of two consecutive months (Table 1 and Fig. 2). Since these mice were not breeding during the period of this irruption they must have been migrating into the area from surrounding territory as conditions improved.

Reithrodontomys is primarily a seed eating species. Furthermore, it probably shows a preference for one seed species over another. It is likely, then, that with a change from a stand of brush, or a grassland of many dominants to a grassland consisting mainly of heavy seed producing annuals, the quantity of preferred food could be one factor to account for the *Reithrodontomys* invasion after cover requirements were satisfied.

The fact that this species did not respond similarly in the burned brush area is probably also due to food quantity. Actual seed production in this area was considerably lower than on the grass area.

Peromyscus maniculatus are also seed eaters, yet they failed to irrupt and remained at a fairly constant density from the time the first year's annuals went to seed. It is possible that their constant low density may be explained on the basis of "home ranges," studied intensively in this region by Brant (1953). According to Dr. Brant, *Peromyscus maniculatus* in local grasslands occupy large home ranges, sometimes several hundred feet in diameter, and tolerate little crowding. Cover requirements of *P. maniculatus* are also different from *Microtus* and *Reithrodontomys.* They are not so dependent on surface runways, but require a more permanent nesting site, such as a deeper burrow, a rock outcrop, or occasional bush. The *Reithrodontomys* occupy smaller home ranges with greater overlap and hence can attain greater density than the *P. maniculatus* on local grasslands.

In brush areas, *P. maniculatus* attain higher densities than in the open grasslands. In the burned brush, conditions apparently enabled these mice to hold their own while undergoing a severe cyclic decline in the unburned brush.

The *Microtus* failed to respond as did the *Reithrodontomys* to conditions of the burn, and reached densities consistent with those on the unburned grassland by the end of the first year's trapping. The reason they did not irrupt in the burned area as did the *Riethrodontomys,* is probably the difference in feeding habits. *Microtus* are generally grass and herb feeders and thus are not so dependent on seeds. Since there was little quantitative change in the new growth after the fire, there was no great increase or decrease in food supply for *Microtus.* All that was necessary for these mice to reestablish themselves was cover. Apparently, on the basis of the results obtained, the floristic change after the fire had little effect on *Microtus.*

As was seen in the brush and in the grassland, *Microtus* were first taken in the late spring of the first year after the fire. They attained approximately the same density on both types of terrain at about the same time. However, even though *Microtus* densities on the burned brush area remained generally consistent with the densities on the burned grass until the spring of the second year, they failed to display the sharp increase shown in the grass areas later during this period.

Feral *Mus* have been reported from this locality before and are not unusual. It appears, however, that certain conditions created by the fire were favorable to these mice. Although only a few were taken on the burned grassland (Table I), enough were taken to warrant mention, especially since none at all were trapped on any other line. Although these mice are far less restricted in their diet than the native species, they are generally known as grain or seed eaters in rural areas (Hall 1927). Therefore, as was the case with the *Reithrodontomys,* it is presumed that the abundance of seeds in the burned grassland accounted for this slight invasion of *Mus*.

Summary

A wild-fire sweeping through a mixed brush and grassland in the Berkeley Hills, essentially annihilated all species of mice, either directly or through removal of food or cover.

In both areas cover seems to be the restricting factor in recovery, especially in the case of *Microtus* which apparently need one year's accumulation of mulch to furnish cover for surface runways.

The change from a grassland of many dominants to one preempted by seed-producing annuals, such as occurred here after the fire, is beneficial to seed eating mice. This was especially found to be the case with *Reithrodontomys,* which irrupted on the burned grass area during a period of seed production during the second winter's growth after cover requirements had been met.

The change from one habitat type (brush) to another habitat type (grass), as happened on the burned brush area, is accompanied by a general species shift from brush dwelling mice to grass dwelling species.

References

Brant, D. 1953. Small rodent population studies near Berkeley, California: *Reithrodontomys, Peromyscus,* and *Microtus*. Unpub. PhD thesis, Univer. Calif., Berkeley.

Calhoun, John B. 1948. North American census of small mammals. Release #1 (Jan.), Rodent Ecology Project, Johns Hopkins Univ., Baltimore, Md.

Fitch, Henry S. 1954. Seasonal acceptance of bait by small mammals. J. Mammalogy **35**: 39-47.

Hall, E. Raymond. 1927. An outbreak of house mice in Kern Co., California. Univ. Calif. Pub. Zool. **30**: 189-203.

Hoffmann, Robert S. 1955. Population fluctuations of small mammals and sooty grouse in California. Unpub. PhD thesis, Univ. Calif., Berkeley.

BEHAVIOR OF CHINOOK AND SILVER SALMON[1]

George H. Allen[2]
Division of Natural Resources, Humboldt State College, Arcata, California

In 1950 the fishway and hatchery ponds shown in Figure 1 were placed into operation at the University of Washington School of Fisheries. This fishway leads into Lake Union, which is connected with Puget Sound about five miles distant via the Lake Washington Ship Canal. With these facilities it is possible to obtain an accurate count of the number of salmon moving daily into the hatchery ponds; consequently, it has been possible to investigate the physical conditions of the environment which are associated with the appearance of the salmon in the ponds. This paper describes some of the physical factors in the environment associated with the movement of silver salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) into the hatchery ponds during the 1953-54 migratory season.

[1] University of Washington, School of Fisheries, Contribution No. 24.

[2] The help of both the University of Washington School of Fisheries and the State of Washington Department of Fisheries, who provided facilities and advice, is gratefully acknowledged.

Description and Operation of Facilities

The fishway, holding ponds, and trap arrangement at the School of Fisheries are shown in Figure 1. The fishway in operation during 1953 consisted of 8 pools with jumps between pools varying from 9 to 11 inches in height. Slots between the pools were one foot wide and spilled water 6 inches deep. The lower 6 pools of plywood construction were 3½ feet wide, 10 feet long, and contained water to a depth of 2 feet. The upper 2 concrete pools were continuous with the lower raceway. The salmon were retained in the lower raceway after passing through a V-type rack. Fish reaching the upper or first pool of the fishway were retained there by a finger-type trap placed at the lower end of the pool. Salmon were prevented from jumping out of the holding pond and trap by a heavy net placed over the arrangement. The water in the fishway originated in the hatchery, which used water pumped from Lake Union and some water from a well.

From October 15, 1953, until March 13, 1954,

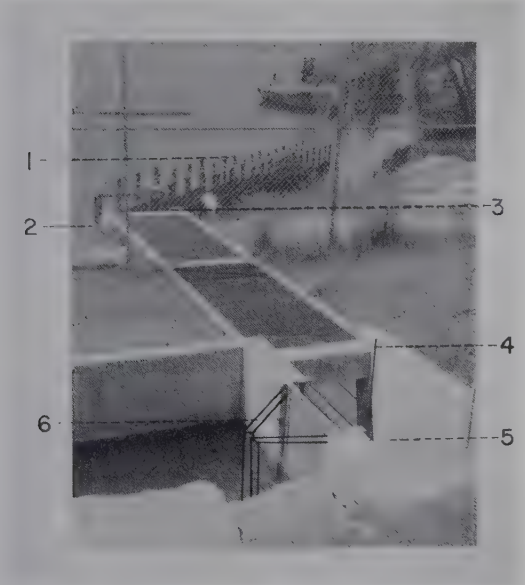


FIG. 1. Fishway and salmon-trapping devices at the University of Washington School of Fisheries
1—Lower pools of plywood construction in use during 1953-54 migratory season.
2—Position of drop board in third pool.
3—Position of baffles, lower end of second pool.
4—Position of baffles, lower end of first pool.
5—Position of finger trap in first pool.
6—Position of V-rack at lower end of raceway.

the trap was examined daily by the first person arriving at the hatchery (usually between 7 a.m. and 9 a.m.). When fish were observed in the trap, a small wire frame was lowered in front of the V-rack, preventing the escape of fish from the trap but not preventing the migration of fish up to the pool below the trap entrance. Sometime during the morning the raceway was lowered and the fishway drained of water. Salmon in the trap were then either killed, spawned, or placed in holding pens.

SALMON RUN TO THE SCHOOL OF FISHERIES IN 1953-54

The composition of the run of salmon to the School of Fisheries during the 1953-54 migratory season is shown in Table I. Prior to October 27, only a few silver-salmon jacks (precocious male) and one chinook-salmon jack entered the traps. The first large chinook, a 3-year-old male, 70 centimeters in fork length, entered on October 27. No chinook salmon appeared after November 20, except one chinook jack arriving on December 1. The first 3-year-old (mature) silver salmon arrived on November 18, with the last 3 appearing

TABLE I. The run of salmon to the School of Fisheries, University of Washington, during the 1953-54 migratory season

Species	Number	Fin Mark	Number	Age
Sockeye....	2	None	2	Not determined
Chinook....	84	None	33	Not determined
		Adipose	48	3 years
		Dorsal	2	2 years (jack)
		RV	1	4 years
Silver.....	151	LV	116	3 years (1950 brood)
		LV	5	2 years (1951 brood, jacks)
		RV	5	2 years (1951 brood, jacks)
		Adipose	22	2 years (1951 brood, jacks)
		None	3	Not determined
Total.....	237			

on February 25, 1954. The peak number of silver salmon arrived during the first week in January.

The sporadic nature of the daily returns made specific studies as to the exact time of movement through the fishway difficult. On November 10 the ponds were visited at 2-hour intervals throughout the night during which time 9 chinook and 2 silver salmon entered. Many other records on the number of fish present in the trap during some particular time of the day were also available. Only a few fish were observed entering the trap during daylight. Most of the fish arrived after midnight, and apparently in the early morning hours of darkness.

In a few cases fish escaped the trap and were caught above the finger-trap of the first pool of the fishway. During the study, 2 instances were recorded of fish completely escaping from both the V-trap and the finger-trap, and leaving the fishway. These occurrences were on days when the trap was not cleared of fish until mid-day. Only 2 fish were found in the fishway below the finger-trap during routine inspection of all pools following emptying of the fishway.

All chinook salmon females were in spawning condition on arrival. Of the 64 three-year-old silver salmon females in the run only 8 were not ripe on arrival. Of these, 4 entered the ponds prior to December 15 and 4 arrived on December 20. All female silver salmon arriving after December 20 were ripe on arrival, except one small female (44 centimeters fork length) spawned on January 5.

In studying the relationship between physical factors and the arrival of silver salmon only the 3-year-old fish marked LV (1950 brood) were considered (Table I). However, 3 LV-marked silver salmon which arrived on February 25 were excluded. The small LV-marked silver salmon of the 1950 brood were separated from the jacks

returning from the LV-marked 1951 brood by the study of lengths, and aging by means of scales. In studying the return of chinook salmon, all returning chinooks except the jacks were considered. A total of 83 chinook salmon and 113 sliver salmon were used in correlating date of return and physical factors in the environment.

Factors Measured and Method of Analysis

The factors measured were as follows: 1. Fluctuation in water level of Lake Washington. The distance from the base of a metal plate on the shore side of the fishway to the surface of the lake was used to measure fluctuations in lake level. 2. Total solar radiation. Data were obtained from the Meteorology Department of the University of Washington, which operated a pyrheliometer on the campus. Total solar radiation is measured by this instrument in Langlies, a unit defined as one gram calorie per minute per square centimeter of horizontal surface. 3. Air temperature. Data were from maximum and minimum thermometers operated by the University of Washington Meteorological Department and the United States Weather Bureau, Federal Building, Seattle. Figures are an average of 4 readings—the maximum and minimum reading from each location. 4. Total daily precipitation. Measurements were from daily readings taken at approximately 4:00 p.m. by the University of Washington Meteorological Department from a rain gauge located in a meteorological tower adjacent to the School of Fisheries. 5. Night-time precipitation (rainfall between 6 p.m. and 6. a.m.). Data were from the United States Weather Bureau, Federal Building, Seattle. 6. Day-time precipitation (rainfall between 6 a.m. and 6 p.m.). Same as 5. 7. Average daily barometric pressure. Data as inches of mercury were from barometers operated by the United States Weather Bureau, Federal Building, Seattle. Figures are an average of 4 daily readings. 8. Temperature of water issuing from base of fishway. Readings were taken daily with a hand mercury thermometer between 4 and 5 p.m. 9. Total daily discharge of water from the Government Locks. The operation of the Lake Washington Ship Canal locks controls the total discharge of water from Lake Washington drainage into Puget Sound. Fishways on the south shore of the dam pass a small portion of the runs; however, most salmon enter through the locks. Total daily discharge from all sources (fishway, spill, and locks) was calculated in cubic feet from records kept by United States government officials operating the locks.

In this type of study there is always the possibility of obtaining a spurious correlation from a trend in time. To minimize such a possibility the following procedure was followed. Fourteen regression lines were calculated by the method of least squares utilizing the values of each physical factor studied against time in days. The deviations from the regression line were used for correlation with the number of fish returning daily rather than the actual value. However, actual values were used in correlating date of return and water discharge from the Government Locks because the extreme variation in the discharge values.

Relative to runs of salmon onto spawning grounds in natural areas, the number of fish involved in the present study was not large. However, this was advantageous in that positive movements separated in time are more susceptible to analysis than large mass-movements in which case stimuli and response are difficult to separate. For silver salmon, there was a large number of days during which no fish or only a single fish appeared. There were only 5 days during which there was a large return of fish, depending on the definition of a large return (Figure 2). Thus the correlation could be thought of as involving only 5 items. Therefore, the correlation coefficients computed were mainly of value in expressing the relative importance of the factors measured, and the graphs were of equal value with the mathematical treatment in interpreting the data.

Results and Discussion

Examination of graphs and correlation coefficients (Table II, and Figures 2 and 3) showed that the movement of the salmon was associated with only one of the physical factors measured: for chinook salmon, falling barometric pressure; and for silver salmon, night-time precipitation.

These results may be interpreted in terms of life-histories of the two species. Fall chinook salmon[3] in the State of Washington generally spawn in the larger rivers where inadequate flows due to lack of rainfall do not usually interfere with spawning. Silver salmon, on the other hand, have become adapted to spawning in small streams where low flows and adverse water temperatures due to lack of autumn or winter rainfall often influence the time and place of spawning. Any behavior in silver salmon adaptive to arrival on the spawning

[3] These are stocks of chinook salmon which migrate from salt water to fresh water during the fall, spawning relatively soon after their arrival on the beds. Spring and summer chinook are stocks entering fresh water during the spring and summer, but not spawning until summer or fall.

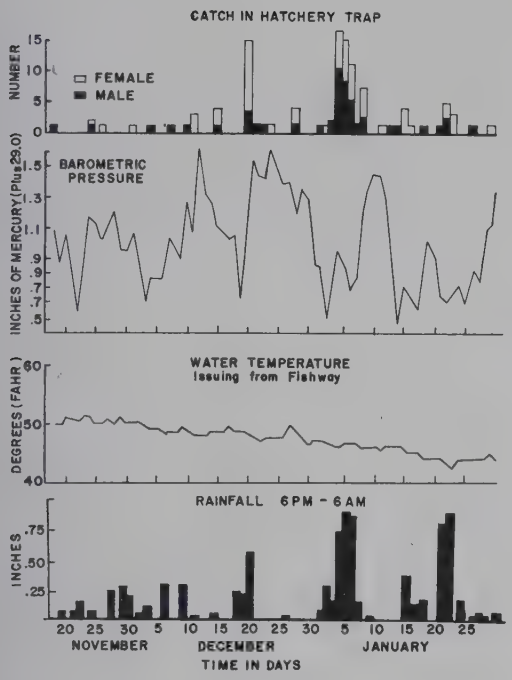


FIG. 2. Daily return of silver salmon to the School of Fisheries during the 1953-54 migratory season compared with meteorologic conditions.

grounds during the time when flow and water temperatures are optimum for spawning would not be unexpected. Such behavior might be exemplified by movement onto the spawning grounds in response to environmental factors associated with increased stream flow, such as rainfall or barometric pressure. Shapovalov and Taft (1954) noted that for silver salmon in Waddell Creek, California, there was a correlation between the general period of the spawning run and the general period of rainfall. However, these authors believed ". . . that there is also a definite relationship between ascension of the stream by spawning fish and *stream flow,* but so far it has proved impossible to show this quantitatively."[4] In the study of silver salmon movements at the School of Fisheries there was no fluctuation in flow and only slight fluctuation in water temperature.

To the author's knowledge, no other predominantly night-time movement of silver salmon in fresh water has been reported in the literature. The acute sense of smell of salmon and the aversion of silver salmon to human scent have been demonstrated by Brett and MacKinnon (1952, 1954). Water in the School of Fisheries fishway could well not have been free of inhibiting

[4] Italics those of Shapovalov and Taft.

TABLE II. Coefficients of correlation between physical factors in the environment and the number of silver and chinook salmon returning to the University of Washington hatchery during the 1953-54 migratory season

Factor	Correlation Coefficient (r)	
	Chinook	Silver
Total Radiation	+.06	−.19
Air Temperature	+.09	+.12
Total Daily Precipitation	−.07	+.30
Day-time Precipitation	−.17	+.06
Night-time Precipitation	+.16	+.63
Barometric Pressure	−.50	−.20
Water Temperature	+.03	+.11
Water Discharge, Gov't Locks	+.27	+.20
N	28	76
Degrees of Freedom	26	74
1% Level of Significance	.49	.29

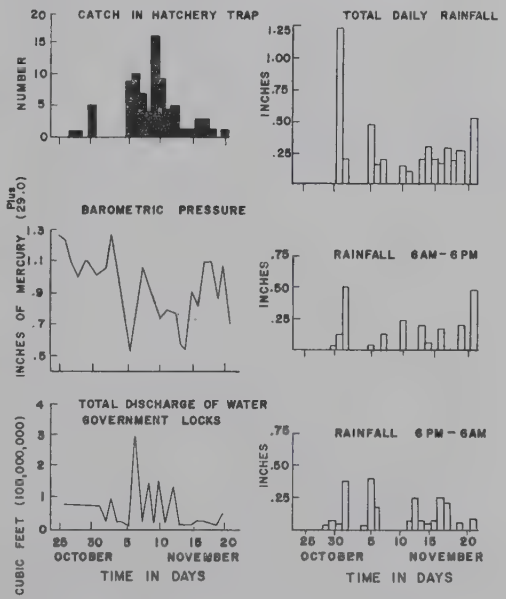


FIG. 3. Daily return of chinook salmon to the School of Fisheries during the 1953-54 migratory season compared with environmental factors.

odors until early evening. The approach to the fishway, however, is quite shallow so that during the day the salmon are fully exposed to both pedestrian and automobile traffic passing to the rear of the fisheries building.

The temperature of the water in the fishway is directly related to the temperature of the water in Lake Union, from which the hatchery water supply is taken. During 1953, silver salmon runs to the streams in the Lake Washington drainage were virtually over by the end of November, whereas the silver salmon run to the School of

Fisheries ponds did not occur until late December and early January. The silver salmon run did not occur until the water temperature had dropped below 50 degrees Fahrenheit. Comparable water temperatures occurred in the natural streams during November. This behavior in relation to temperature is similar to that reported for sockeye salmon (*O. nerka*) in the Fraser River, British Columbia, Canada, by Royal (1953).

All of the salmon involved in the present study were hatched and reared in fish cultural stations in the State of Washington, then transferred to the School of Fisheries for marking, and release. The return of the salmon to the point of release must be considered as conditioned behavior (Donaldson and Allen 1958). However, as the fish had no opportunity to become conditioned to natural stream gravels, the movement into the ponds, which I consider analogous to movement onto the spawning beds in natural areas, must be considered as innate behavior in the sense discussed by Tinbergen (1951). That these adult fish would have spawned if natural conditions were available has been established repeatedly by many salmon marking and transplanting experiments in Canada, the United States and elsewhere. Following Hoar (1953) it is suggested that the movement of the salmon into the ponds represented a low level of appetitive behavior, if not actually a consummatory act, in the hierarchical arrangement of the homing instinct in salmon.

The delay of entry into the ponds by the silver salmon due to high water temperatures, and the advanced state of maturity of the fish on arrival into the ponds, may be considered in terms of appetitive and consummatory behavior (Thorpe 1957, Tinbergen, and Hoar *loc. cit.*). In the relatively warm water, stimuli furnished by the external environment were inadequate to initiate movement into the ponds, that is, to trigger an innate releasing mechanism. Advancing sexual maturity and lower water temperatures lowered the threshold of response so that previously inadequate stimuli finally did initiate movement into the ponds. The night-time movement was probably directed by internal stimuli.

The behavior of the salmon is consistent with the concept that consummatory acts or appetitive behavior of low order are increasingly susceptible to initiation by external stimuli. If the idea is valid that certain behavior can result from a heterogeneous summation of stimuli, there is the possibility that for the silver salmon, as well as for the chinook salmon, barometric pressure was involved in stimulating the movement into the ponds because a sharply dropping barometric pressure preceded each large return. What specific physiological or psychological mechanisms were involved is not known.

For the Pacific salmon it is likely that available physical features on the spawning grounds orient the choice of a spawning location and that other stimuli direct the reproductive behavior from that point. These relationships for Pacific salmon have not been critically studied as yet in terms of the new approach to animal behavior as advocated by Tinbergen, Hoar, Thorpe and others.

Summary

Artificial runs of silver salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) were established in the fall of 1951 at the University of Washington School of Fisheries with the completion of new hatchery and fishway facilities in 1950. It is simple to obtain a daily count of fish returning to the hatchery ponds, and therefore to study the physical conditions of the environment associated with the appearance of the fish in the ponds. During the fall of 1953 and winter of 1954 a total of 237 salmon were trapped at the hatchery ponds. Of these, 83 chinook salmon and 113 silver salmon were used in correlating the date of return and certain physical factors in the environment. A uniform flow of water in the fishway was maintained by a water supply taken mainly from the environment in which the salmon were resting prior to movement into ponds through the fishway. Movement of silver salmon into the ponds was correlated with night-time rainfall. Movement of chinook salmon corresponded with periods of low barometric pressure. The movement into the ponds were analogous to movement onto the spawning beds in natural areas. The movement was considered innate behavior because all of the fish involved in the study were never conditioned to natural stream gravels. This observed behavior was discussed in terms of the recent approaches to animal behavior advocated by Tinbergen (1951), Hoar (1953), and Thorpe (1957).

References

Allen, George H. 1956. Migration, distribution, and movement of Puget Sound silver salmon. Doctoral Thesis, University of Washington.

Brett, J. R., and D. MacKinnon. 1952. Some observations on olfactory perception in migrating adult coho and spring salmon. Fish. Res. Bd. Canada, Prog. Repts. Pac. Coast Sta's., No. **90**: 21-23.

———. 1954. Some aspects of olfactory perception in migrating adult coho and spring salmon. J. Fish. Res. Bd. Canada, **11**: 310-318.

Donaldson, L. R. and G. H. Allen. 1958. Return of silver salmon, *Oncorhynchus kisutch* (Walbaum), to point of release. Trans. Amer. Fish. Soc. Vol. 87 (1957) : 13-22.

Hoar, W. S. 1953. Control and timing of fish migration. Biol. Rev. Cambridge Philo. Soc., **28**(4) : 437-452.

Royal, L. 1953. The effects of regulatory selectivity on the productivity of Fraser River sockeye. Canadian Fish Culturist, No. **14**: 1-12.

Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California. Calif. Div. Fish and Game, Fish. Bull No. **98.**

Tinbergen, N. 1951. The Study of Instinct. Oxford, Clarendon Press.

Thorpe, W. H. 1957. Some implications of the study of animal behavior. The Scientific Monthly, **84**: 309-320.

SHELL FORMATION AND GROWTH OF THE CALIFORNIA XANTHID CRABS

Jens W. Knudsen
Department of Biology Pacific Lutheran College, Parkland, Washington

Introduction

This paper deals with the post-exuvial sclerotization, or shell deposition, as it is related to the early phase of the intermolt cycle of *Cycloxanthops novemdentatus* (Lockington), and with the size increment at the time of molting of the major California Xanthidae, the pebble crabs. Xanthid crabs are typically found in tropical waters and are represented in California by only 5 genera. Of these only *Lophopanopeus, Cycloxanthops,* and *Paraxanthias* are abundant intertidally, the other 2 genera are either highly restricted in distribution or absent at this time. The biology of the family Xanthidae was studied by the writer while at the Allan Hancock Foundation, University of Southern California, Los Angeles 7, California.

The intermolt cycle begins immediately after ecdysis and includes all of the physiological changes that are essential to continued growth. It begins with endysis (the act of developing a new coat) and ends with the resorption of salts from the shell in preparation for ecdysis. Olmstead and Baumberger (1923) were the first to study the "molt cycle" as such. They assigned 6 stages which they called (1) "hard," (2) "pillans," (3) "about to molt," (4) "newly molted," (5) "soft," and (6) "paper shell." Their criteria, however, were based on osmotic pressure, water content, freezing point and other features that do not readily lend themselves to work with living animals. Drach (1939, 1944, 1947), after an extensive study of the intermolt physiology and changes in blood chemistry of *Maia squindo* Herbst and *Cancer pagurus* Linné, worked out a system where the stages of the intermolt cycle can be determined by visible morphological changes in the crab. Hiatt (1948) worked out the intermolt cycle of *Pachygrapsus crassipes* Randall using a modification of the system set forth by Drach. The present paper follows the method of Hiatt and deals only with the first phase of the intermolt cycle, that of endysis. It supplements the information contributed by Drach on an oxyrhynchoid and a cancroid crab, and that of Hiatt on a grapsoid crab, in that it extends our knowledge to the family Xanthidae. Likewise, the study of growth and size increment follow a standard method, as used by Hiatt (1948) and others, but it also extends the present knowledge of the Brachyura to the Xanthidae.

Endysis and the Intermolt Cycle

In this study the course of endysis was plotted daily for 6 post-exuvial specimens of *Cycloxanthops novemdentatus.* This process was not mapped to completion, but the data obtained shed light on the family Xanthidae. Table I gives a summary of the post-exuvial sclerotization for the 6 individuals, averaged for a period of 17 days. Of extreme interest is the fact that all areas exposed to attack by predators harden first. Those areas which receive protection from the rocky crevice in which the crab hides, or from other body parts, harden more slowly.

Within 2 hours after ecdysis there is a very noticeable deposition of salts around the breaking plane of the pereiopods. At 4 hours there are enough salts present to allow autotomy. In 8 hours this area (basi-ischium) is completely hard and cannot be depressed without crushing the segments. This allows the xanthid crab to autotomize an appendage if attacked, and greatly enhances the chances for survival. Neither Drach (1939) nor Hiatt (1948) mention the rapid process of sclerotization in the basi-ischium but both speak of autotomy after ecdysis. Thus, it is probably universal for all Brachyura.

TABLE I. ABBREVIATIONS: Prog., progastric area; M & U G., Meso- and urogastric area; Ant. Br., anterior branchial area; Post. Br., posterior branchial area; Ant. Epi., anterior epibranchial area; Post. Epi., posterior epibranchial area; Card. Area, cardiac area; Thor. St., thoracic sternites; Carp., carpus; Prop., propodus; Dact., dactylus.

SYMBOLS: xxxx, integument completely soft; xxx, integument firm; xx, integument partially rigid but easily depressed; x, integument partially rigid but somewhat depressible; 0, integument rigid but thin, and easily broken; –, integument completely rigid, not easily broken.

TABLE I. Post-exuvial sclerotization of six *Cycloxanthops novemdentatus*

Day	Carapace							
	Prog.	M & U G.	Ant. Br.	Post. Br.	Ant. Epi.	Post. Epi.	Card. Area	Thor. St.
1	xxx	xxx	xxx	xxx	xxx	xxxx	xxxx	xxxx
2	xx	xx	xx	xx	xx	xxx	xxx	xxxx
3	x	xx	x	xx	xx	xx	xx	xx
4	x	xx	x	xx	x	xx	xx	xx
5	x	xx	x	xx	x	xx	xx	xx
6	x	xx	x	xx	x	xx	xx	xx
7	0	xx	x	xx	x	xx	xx	xx
8	0	x	0	x	x	xx	xx	xx
9	0	x	0	x	x	xx	xx	xx
10	0	x	0	x	x	xx	xx	xx
11	0	x	0	x	x	xx	xx	xx
12	0	0	0	x	0	xx	x	xx
13	0	0	0	x	0	xx	x	xx
14	0	0	0	x	0	xx	x	xx
15	–	0	0	0	0	x	0	xx
16	–	0	0	0	0	x	0	x
17	–	–	–	–	0	x	0	x

Day	Chelae				Walking Legs			
	Claws	Palm	Carp.	Merus	Merus	Carp.	Prop.	Dact.
1	xxxx	xxx	xxx	xxx	xx	xx	xx	xx
2	xxxx	xxx	xx	xxx	xx	xx	xx	xx
3	xxxx	xxx	xx	xxx	x	x	x	x
4	xxx	xx	x	xxx	x	x	x	x
5	xxx	x	0	xx	x	x	x	x
6	xx	x	0	xx	x	x	x	x
7	xx	x	0	xx	x	x	x	x
8	x	0	0	x	x	x	x	x
9	0	0	0	x	x	x	x	x
10	0	0	0	0	x	x	x	0
11	0	0	0	0	x	x	x	0
12	0	0	0	0	x	0	0	0
13	0	0	0	0	x	0	0	0
14	0	0	–	0	x	0	0	0
15	–	–	–	0	x	0	0	0
16	–	–	–	–	0	0	0	–
17	–	–	–	–	0	–	–	–

The frontal, orbital, and anterolateral margins of the carapace are next to receive salts. Likewise, the dorsal area of the carapace and propodus of the chelae are quickly impregnated with lime salts. However, the ventral areas of the chelae and posterior areas of the carapace remain soft and flexible for a greater length of time. Hiatt mentions that *Pachygrapsus crassipes* will attempt to use its chela as early as 4 days after ecdysis but cannot pinch normally until 10 days have elapsed. With *Cycloxanthops novemdentatus* the claws receive very little salts early in endysis. A very thin brittle layer is deposited about the fourth day, but there is no strength in the claws until the tenth day. At this time the claws are still easily damaged if not protected, and the crab makes no attempt to use them. At about the twelfth day the xanthid crab begins to open its claws, but does not try to pinch with any force until several days later. Thus the xanthid crab is sclerotized in a manner which gives the maximum protection from danger but does not allow any real offensive activity.

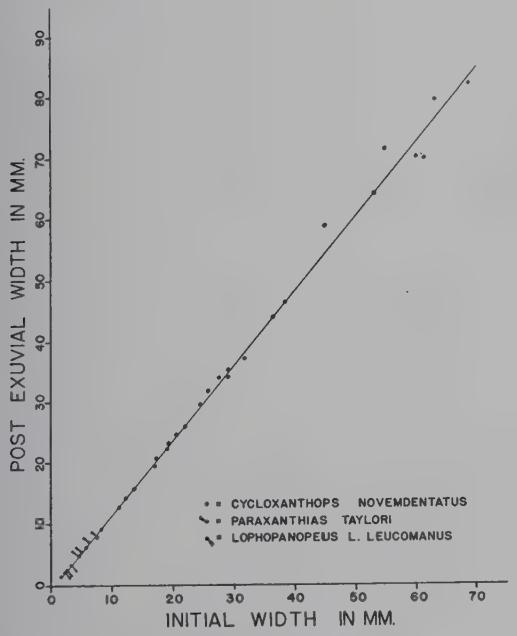
It seems of particular interest that the stomachs of recently molted xanthid crabs, which were examined in the field, contained mostly coralline algae. An examination of the intestinal contents revealed that the larger segments of algae were reduced to a fine granular substance, either by mechanical grinding in the stomach, or by chemical reduction in the intestine. Coralline algae of the species *Corallina gracilis* Lamouroux, *Corallina vancourverensis* Yendo, *Bossia orbigniana* (Decaisne) Manza, and *Bossia gardneri* Manza were found abundantly in the spaces used for molting by *Cycloxanthops novemdentatus* and *Lophopanopeus l. leucomanus*, and growing near the hiding places of *Paraxanthias taylori*. Since the lime salts in the xanthid shell and in the coralline algae are similar it appears probable that the algae is used as a source of shell material. To test this in the laboratory, coralline algae was fed to one group of post-molt xanthid crabs while another group was fed on non-coralline red algae. Crabs which were fed on the former hardened faster and produced thicker shells than those fed on the latter algae. Thus, the small amount of data available suggests that coralline algae may be directly broken down, and the salts used in endysis.

A further study of endysis was rendered impractical without marine-laboratory facilities. The intermolt cycle involves not only morphological changes, but also the time necessary to complete these changes. It is necessary, therefore, to maintain animals under natural conditions for long periods of time in order to get a true measurement of the changes as they would occur in nature. Such data are then useful in determining the age of individuals as well as in explaining their physiological activity between molts.

Growth, Size Increment, and Age

The size increment at ecdysis is the best indicator of growth. The newly formed carapace of an individual represents the external size to which the crab will ultimately grow internally before the next ecdysis. A total of 33 xanthid crabs that went through ecdysis in the laboratory were measured for size increment.

Figure 1 shows the initial width plotted against the post-exuvial width. The crabs represented are males more than 12 millimeters wide, or juveniles, with the exception of one 25 millimeter, pre-exuvial, female *Cycloxanthops novemdentatus*.



SIZE INCREMENT AT ECDYSIS

Fig. 1. This shows the new carapace width after molting plotted against the initial carapace width prior to molting, whereby the number of molts required to reach a given carapace size may be determined.

After the graph for this species was made, the growth rate for *Paraxanthias taylori* and *Lophopanopeus l. leucomanus* was found to be identical and so was plotted on the same graph.

When the size of a small individual is fitted to the initial-size margin, the expected post-exuvial size can quickly be obtained, as can the number of molts necessary to reach a particular size. By beginning with the initial width of the first crab stage the post-exuvial width can be obtained. Now, if the post-exuvial width is again fitted to the initial-width margin a second post-exuvial width is obtained. This process is repeated until the desired post-exuvial width is reached. Thus, a 19 millimeter *Lophopanopeus l. leucomanus* required about 20 molts to reach that size while a 42 millimeter *Paraxanthias taylori* required about 25 molts. The largest male *Cycloxanthops novemdentatus* known, a 100 millimeter specimen collected by the writer, probably required only 29 molts to reach its size.

The age of individual xanthid crabs could be plotted if more were known about the frequency of molting or the time involved in the intermolt cycle. Data are lacking here, however, thus making any such estimate pure conjecture.

Summary

1. The shell formation of a representative xanthid crab, *Cycloxanthops novemdentatus,* has been tabulated for a period of 17 days. It has been shown that those areas of the shell which may be exposed to attack by an enemy, harden first. Areas which are protected by the rocky crevice in which the crab hides, or by other body parts, harden more slowly.

2. The fracture plane of all pereiopods harden with extreme rapidity, being hard enough in 4 hours to permit autotomy to occur.

3. Field and laboratory data suggest that coralline algae is used by xanthid crabs as a source of shell salts, and show that shell formation is accelerated when coralline algae is in the diet of the crab.

4. Size increment at the time of molting has been plotted against the initial size of the 3 xanthid genera, thus making it possible to estimate the number of molts necessary to reach a given body size. Sufficient data are lacking, with reference to the time required during the intermolt cycle, to estimate age.

References

Drach, P. 1939. Mue et cycle d'intermue chez les Crustacès décapodes. Ann. de L'Inst. Océano., NS **19**: 106-377.

———. 1944. Etude préliminaire sur le cycle d'intermau et son conditionnement hormonal chez *Léander serratus* (Pennant). Bull. Biol. de la France, **78**: 40-62.

———. 1947. Lumière, glande de sinus et vilesse de Parcours des intermues chez *Léander serratus* (Pennant). Compt. Rend. Acad. des Sci., **228**: 1563-1565.

Hiatt, R. W. 1948. The biology of the lined shore crab, *Pachygrapsus crassipes*. Randall. Pac. Sci., **2**: 134-213.

Olmstead, J. M. D., & Baumberger, J. P. 1923. Form form of three species of grapsoid crabs and their growth at molting. Jour. Morph., **38**: 279-294.
and growth of grapsoid crabs. A comparison of the

SEASONAL DISTRIBUTION AND SETTLING RATES OF ESTUARINE BRYOZOA[1]

FRANK J. S. MATURO, JR.[2]
Department of Zoology, Duke University, Durham, North Carolina

Records of the seasonal distribution and reproductive periods of the Bryozoa are sparse. Much of the available information is based on the finding of ovicelled specimens in dated collections; however, better information is to be had from the few test panel studies which include reports on the more common bryozoans of marine fouling communities. The latter method also permits analysis of larval settling rates and factors involved in the selection of attachment sites. Comprehensive reviews on the test panel studies have been presented by McDougall (1943) and the Woods Hole Oceanographic Institution (1952).

Several factors have been found important in connection with bryozoan settling in seasonal studies. Visscher (1927) has demonstrated the importance of dark surfaces for collecting panels, Pomerat and Weiss (1946) have pointed out the effects of surface texture, while Pomerat and Reiner (1942) and McDougall (1943) have shown the influence of substrate angle and light on the attachment of sedentary organisms.

The present paper deals with test surface studies on the Bryozoa specifically, utilizing a combination of the techniques of the above workers. It is the purpose of this study to report on the seasonal distribution, spatial distribution, reproductive periods and settling rates of estuarine bryozoans at Beaufort, North Carolina, with a consideration of environmental factors related to these. Other ecological observations on these species have been presented earlier (Maturo 1957).

The writer wishes to express his sincere appreciation to Dr. I. E. Gray, under whose guidance this work was done. Thanks are also due to Dr. C. G. Bookhout for placing the many facilities of the Duke University Marine Laboratory at the writer's disposal, and to the U. S. Coast Guard and U. S. Army Corps of Engineers for permission to use permanent pile markers at investigation sites.

METHODS

Three stations were established in the vicinity of Beaufort, North Carolina, the sites being selected on the basis of ecological differences and convenience of location. At each station an experimental piling was erected which consisted of two parallel 2 × 4" untreated pine beams 16 feet in length, between which was placed a series of 3 × 6 × ¾" unglazed ceramic tiles (identical with those selected by McDougall). The tiles were set in groups of 3 which were distributed at intervals of 2 feet along the piling in such a manner that the first set was at a point corresponding to the low tide mark and the last set at the bottom. Each tile in a set was separated from its neighbor by an inch and a half interval. Members of a set were oriented so that the first tile was vertical, the second horizontal, and the third at a 45° angle. Thus a series of angles, 0° (undersurface of horizontal tile), 45° (undersurface of angle tile), 90° (vertical tile), 135° (upper surface of angle tile), and 180° (upper surface of horizontal tile), was available at each depth interval on which larvae could settle. All tiles were numbered with black paint to indicate station number, depth level, and orientation.

Tiles were collected at 2-week intervals from May, 1954, to May, 1955. At these times a piling was brought on the deck of a boat and the tiles rapidly removed to a rack submerged in a tank of fresh sea water. The piling was then scraped clean of fouling organisms and a clean set of tiles was set into it, after which the structure was returned to the water and secured. Surface and bottom water temperatures, water samples for salinity determinations, and Secchi disc readings were taken at each visit. Current measurements were made at the 3 stations during August 4-6, 1955.

All bryozoans on the tiles were counted, the species and number being recorded according to tile number and surface. Settling rates were calculated by the method employed by McDougall (1943).

Physical Characteristics of the Three Experimental Stations

Despite the rather close proximity of the localities selected for study, the nature of the coast and local channels presents certain environmental differences (Figure 1). Station 1 is located in the Newport River estuary at a point where the channels from Beaufort and Morehead City converge. The shallow estuary has mainly a mud bottom with numerous oyster reefs and marginal *Spartina* marshes, although large stretches of sandy shoals

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[2] Author's present address: Department of Biological Science, University of Florida, Gainesville, Florida.

FIG. 1. Map of the immediate vicinity of Beaufort, North Carolina, with the locations of the three stations and notations on the bottom types.

comprise the lower middle portion along the Intracoastal Waterway. Station 1 is situated in the channel where the depth is 11 feet (mean low water), whereas the remainder of the basin averages less than 5 feet at low tide.

Station 2 is located in Bogue Sound in front of Morehead City at a distance of 2.7 miles from Beaufort Inlet. The area has a sand and shell bottom with very shallow waters except for the channel which is maintained at 12 feet. The station is situated between shoals and flats exposed at low tide and the channel in a depth of 9 feet. Most of Bogue sound, including this portion, is so situated that drainage from the Newport River estuary does not enter it, but rather is diverted directly toward the inlet.

The Duke Marine Laboratory pier in Beaufort harbor is the location of Station 3. During ebb tide the harbor receives part of the drainage from Newport River, whereas flood tide brings in water directly from the inlet. Although the harbor is 12 feet deep, the depth at the station site is 9 feet at low tide. The bottom here is sand and mud.

The temperature readings for the three stations are essentially identical as is shown in Figure 2. These water temperatures follow closely the average monthly air temperatures for Morehead City as prepared by the U. S. Department of Commerce Weather Bureau (1954 and 1955). For comparison are mean water temperatures for 1924-1928 and 1941-1942 as reported by Gutsell (1930) and McDougall (1943), respectively, for the same locality as Station 3.

Figure 3 shows the salinity for the stations at low tide at two-week intervals. The range and fluctuation of salinity at Station 1 are much greater than those of the other stations. Station 2 exhibits a high degree of stability within a narrow range of high salinity while Station 3 appears intermediate between the other two. Temperature and salinity stratification are nil at the station sites.

Tidal current rates at Station 1 were found to be a maximum of 0.7 feet per second at the surface. However, it was observed that there were long periods of time during the tidal cycle in which there was practically no current. Apparently the divergence or convergence (depending on the direction of flow) of the tidal currents above the station establishes a slack water area in the immediate vicinity during most of the tidal cycle. Water at Station 3 was found to be in rather constant movement with a maximum speed of 1 foot per second although occasional rates of 1.5 feet per second (McDougall 1943) might be reached. Tidal currents at Station 2 were observed to be maintained for long periods of time at a much higher rate than that recorded for the other stations. Here the maximum rate was found to be 3.2 feet per second, a speed which persisted for a little over 2 hours during a tidal cycle. Slightly lower speeds which were still above the maxima of the other stations were recorded for the remainder of the cycle with the exception of the Secchi disc readings being mostly less than 6 feet.

Estuarine waters at Beaufort are quite turbid, slack water periods.

RESULTS

Bugula neritina (Linnaeus)

Of the 19 species of bryozoans which settled on the tiles *Bugula neritina* was by far the commonest. This species reproduced in the Beaufort area practically all year long, with the exception of the colder months of January, February, and March. Larval settlement began about the first of April and continued through the third week of December.

Figure 4 shows the seasonal distribution of *B. neritina* at Station 1. The greatest settling of larvae on the experimental tiles took place during the last half of June with numbers declining gradually through the summer until the second week of October. Then a sharp rise occurred which

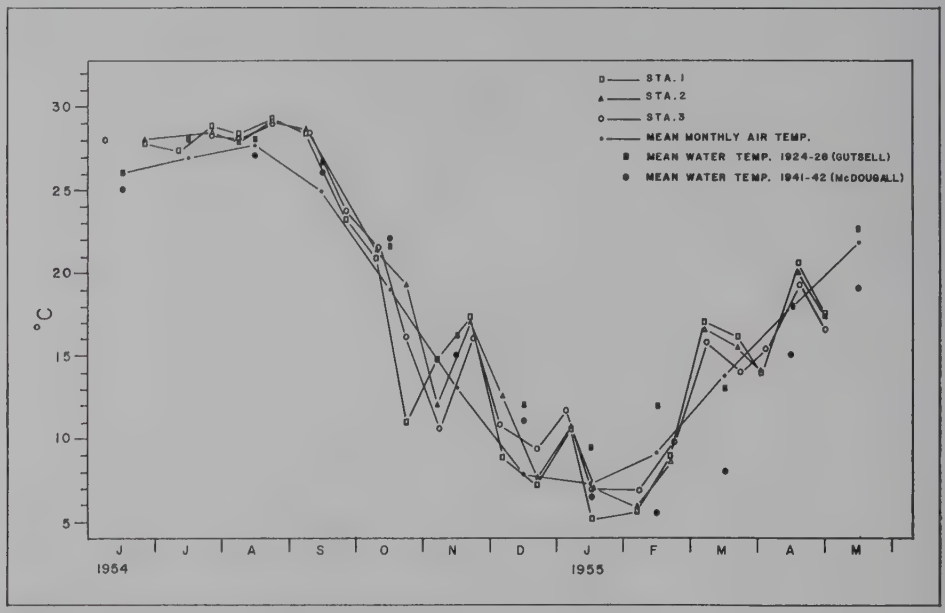


FIG. 2. Surface water temperatures at the three stations from June, 1954, to May, 1955. Readings were taken at two-week intervals during low tide periods. Also plotted are mean monthly air temperatures for the same period and mean water temperatures reported by Gutsell (1930) and McDougall (1943).

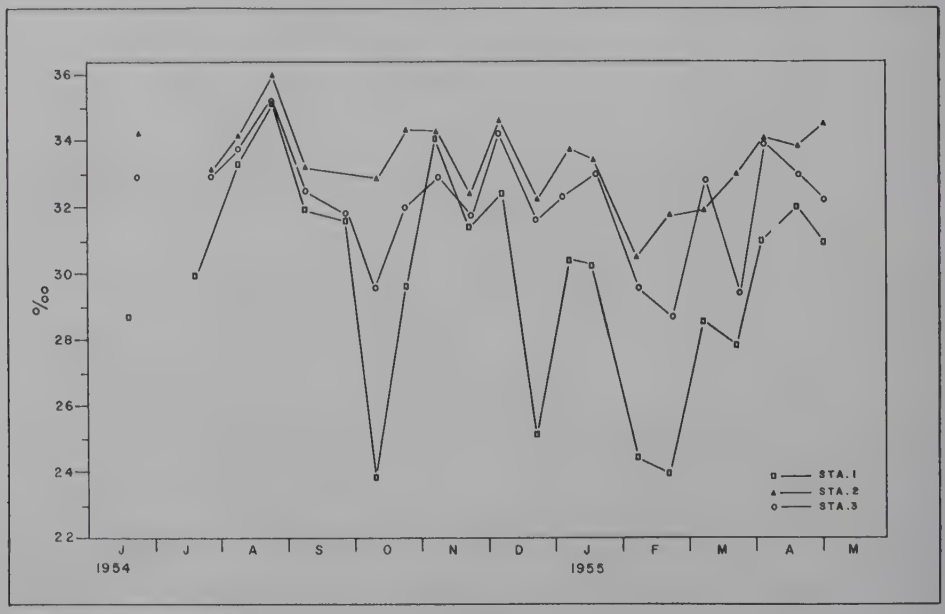


FIG. 3. Salinity of surface water at the three stations from June, 1954, to May, 1955. Readings were made at two-week intervals during low tide periods.

persisted until early November, thus marking a second seasonal peak somewhat less pronounced than that in June. The peaks occur at Station 2 (Figure 5) at approximately the same times as those at Station 1; however, a striking difference is noted in the numbers comprising these peaks.

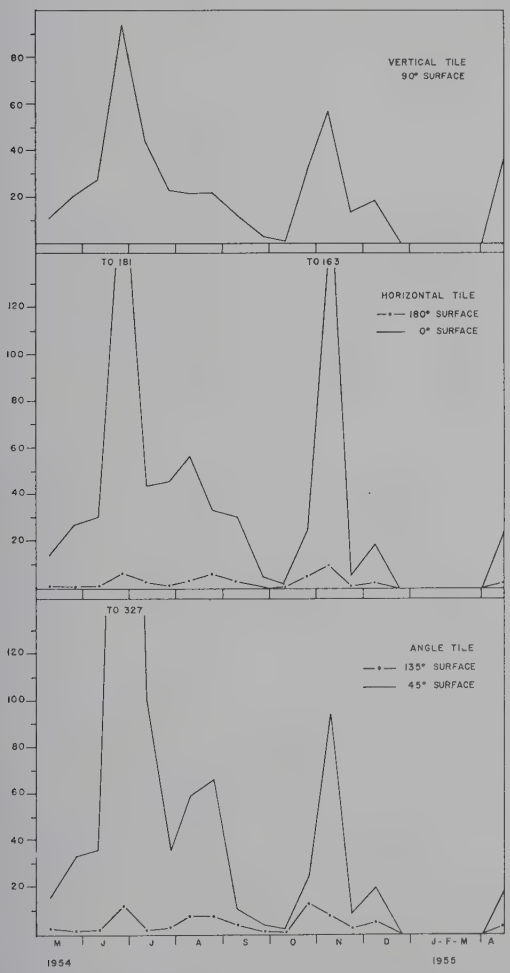


FIG. 4. Seasonal distribution, settling rates, and surface orientation "preference" of *Bugula neritina* at Station 1. Number of larvae that settled per tile (3 × 6 inches) per week.

From Figure 6 it can be seen that Station 3 presents an intermediate picture as far as the number of settlings is concerned. In addition the first setting peak is divided such that larger numbers were recorded in mid-May with a second peak occurring in late June which corresponds to the times of maximum larval settlement at the other two stations. Thereafter only minor fluctuations were recorded at a lower population level.

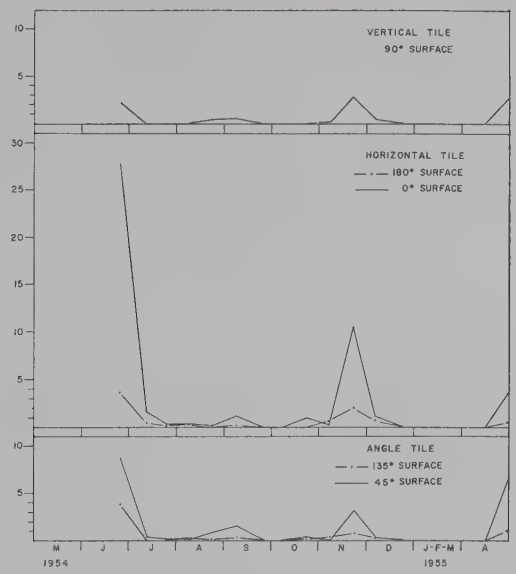


FIG. 5. Seasonal distribution, settling rates, and surface orientation "preference" of *Bugula neritina* at Station 2. Number of larvae that settled per tile (3 × 6 inches) per week. (Data missing from May 9 to June 11, 1954, due to vandalism.)

TABLE I. Numbers of *Bugula neritina* larvae that settled at various depths below low tide level at the three stations during the summer

Station	1	3	2
Date	6/9-8/21/54	6/8-8/22/54	6/11-8/21/54
Depth in feet	Number of Larvae		
0- 1	1960	121	23
2- 3	3996	652	199
4- 5	4121	689	121
6- 7	3249	654	145
8- 9	1721	835	22
10-11	662		

The vertical distribution of larval settlement at the three stations is shown in Table I. The numbers of larvae settling recorded for each depth interval represent the total numbers on the 5 variously oriented surfaces at the given depths. Certain differences in the 3 localities are evident. The greatest settling of *Bugula neritina* larvae occurred at Station 1 and in numbers consistently larger than the other stations. Stations 3 and 2 had respectively smaller numbers of larvae settling.

At Station 1 the numbers of larvae which settled increased from the low tide level down to about 5 feet, then progressively decreased toward the bottom. However, during times of marked salinity drops a different distribution picture was observed. At these times few larvae settled near

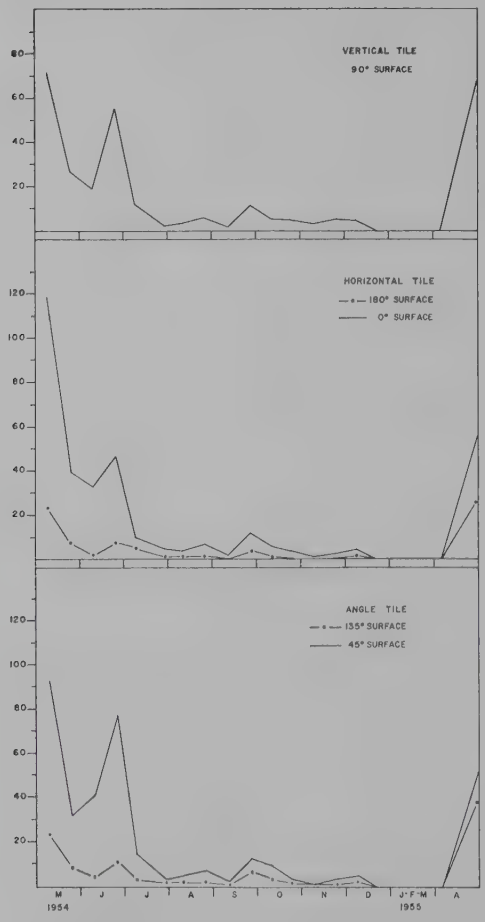


FIG. 6. Seasonal distribution, settling rates, and surface orientation "preference" of *Bugula neritina* at Station 3. Number of larvae that settled per tile (3 × 6 inches) per week.

the surface, the numbers tending to increase gradually to mid-depths, then increase rapidly toward the bottom.

Station 3 at the Duke pier presented a rather regular vertical distribution pattern. After a sharp increase in larval settling from the surface to about 3 feet, the numbers remained about equal at the various depth intervals with a general tendency toward an increase with depth. If only the settling on the vertical surfaces is considered, a very clear-cut picture of numbers increasing with depth is obtained.

The data on vertical distribution at Station 2 are very erratic because of the low numbers of larvae which settled. Most of the numbers of larval settlement reported for this station in Table I occurred during one observation period in June. Little can be learned from an analysis here except that tiles just below the surface and at the bottom are apparently much less preferred than the others.

As described elsewhere, 3 tiles were set in the experimental piling at each two foot depth interval such that one tile was vertical, another horizontal, and the third was at a 45° angle. It was found that almost invariably the 0° and 45° surfaces had the highest numbers of *B. neritina* larvae settling on them at all depths (Figures 4, 5, and 6). Next in order of decreasing numbers were 90°, 135°, and 180°. The difference in the numbers of larvae settling on the 0°, 45°, and 90° surfaces as compared to the 135° and 180° tiles is particularly noticeable during the seasonal peaks, especially at Stations 1 and 3. These latter two surfaces accumulated rather thick layers of sediments and could immediately be distinguished from other tiles in a set from an experimental piling.

Schizoporella unicornis (Johnston)

This species was the most abundant of the encrusting forms found on the experimental tiles. Settlement of larvae occurred throughout the year with the exception of January, February, and March. As was the case with *Bugula neritina*, young colonies appeared during the first half of April at Stations 1 and 3, and 2 weeks later at Station 2.

Rather startling results concerning the seasonal peaks and relative abundance of set are recorded in Figures 7, 8, and 9. It should be pointed out that Figures 8 and 9 are on a different scale from Figure 7 because of the low numbers obtained at Stations 2 and 3. Settling of larvae in Newport River at Station 1 was consistently greater than at the other 2 stations. Though *S. unicornis* was settling at Station 1 in May and June in sufficient numbers to constitute a peak corresponding to those at Stations 2 and 3, the obvious peaks occurred in August and November. Peak settlement took place during June and September in Beaufort Harbor, while settling in Bogue Sound lagged about 2 weeks behind with the first peak emphasized.

The vertical distribution of *S. unicornis* on the tiles was found to be quite variable (Table II). However, at Stations 1 and 3 the last (deepest) set of tiles on each piling was colonized by at least 3 times as many larvae as most other sets of tiles on the basis of total settling counts for the summer months. Station 2 differed in that settling increased from the surface down to mid-depths (4-5 feet) and then decreased again to the bottom.

Like *Bugula neritina*, *Schizoporella unicornis* exhibited a substratum orientation preference in

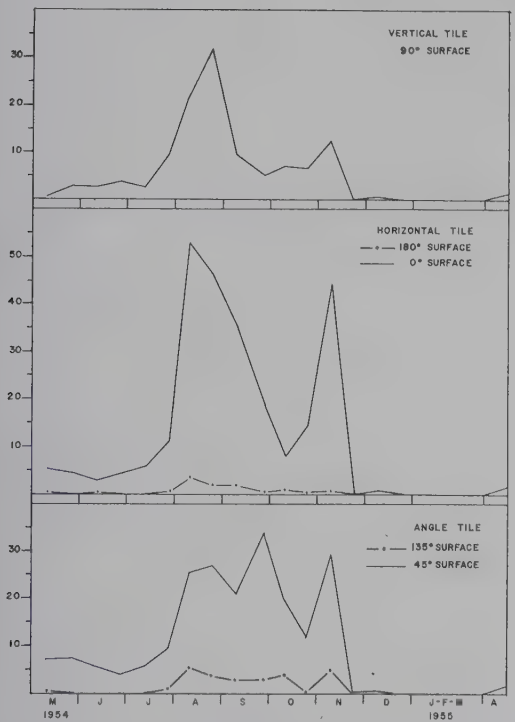


FIG. 7. Seasonal distribution, settling rates, and surface orientation 'preference" of *Schizoporella unicornis* at Station 1. Number of larvae that settled per tile (3 × 6 inches) per week.

TABLE II. Numbers of *Schizoporella unicornis* larvae that settled at various depths below low tide level at the three stations during the summer

Station	1	3	2
Date	6/9-8/21/54	6/8-8/22/54	6/11-8/21/54
Depth in feet	Number of Larvae		
0- 1	277	11	10
2- 3	61	72	56
4- 5	590	28	97
6- 7	447	55	25
8- 9	568	173	18
10-11	1458		

which the 0° and 45° tiles were most heavily colonized, with decreasing settling on 90°, 135°, and 180° surfaces, respectively (Figures 7, 8, and 9). Results from Station 2 were somewhat erratic, for here the "preference" for 90° and 135° surfaces was usually reversed.

Other Species—The following species occurred on the experimental tiles at various times but were not present in sufficient numbers to treat in the same manner as the two preceding species. The reproductive periods of these, as determined from

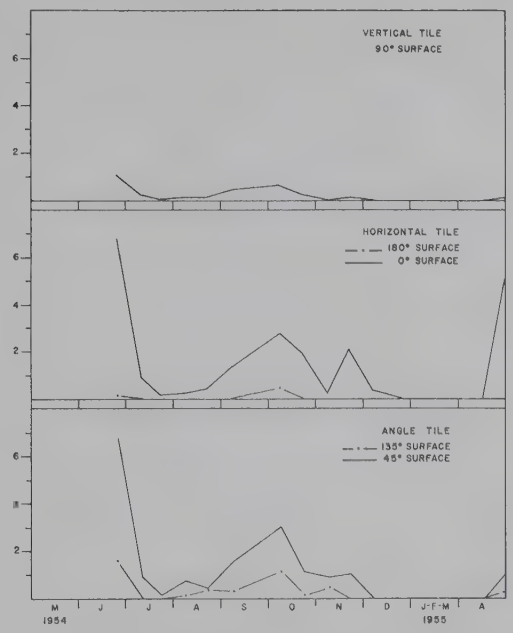


FIG. 8. Seasonal distribution, settling rates, and surface orientation "preference" of *Schizoporella unicornis* at Station 2. Number of larvae that settled per tile (3 × 6 inches) per week. (Data missing May 9 to June 11, 1954, due to vandalism.)

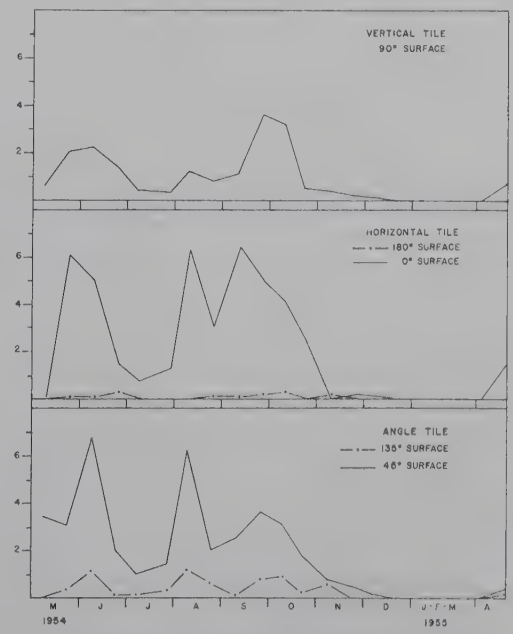


FIG. 9. Seasonal distribution, settling rates, and surface orientation "preference" of *Schizoporella unicornis* at Station 3. Number of larvae that settled per tile (3 × 6 inches) per week.

the piling studies, are shown in Figure 10. The order in which they are considered is systematic rather than in terms of abundance.

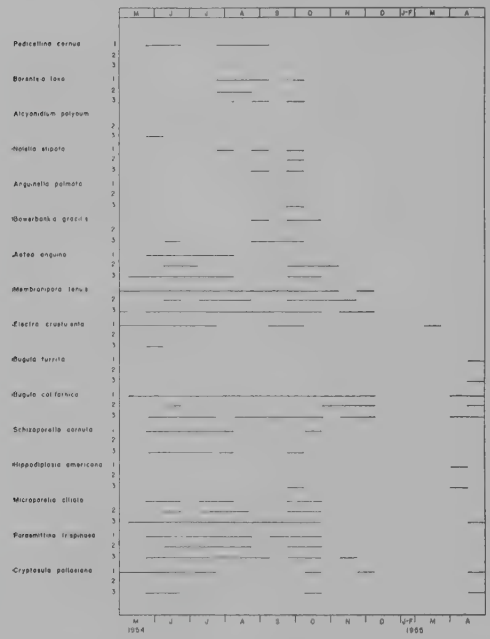


FIG. 10. Reproductive periods of some bryozoans at Beaufort, North Carolina, as determined from the piling studies. May, 1954, through April, 1955. Numbers following each species designate the station for each record.

Pedicellina cernua (Pallas)

This inconspicuous entoproct settled on the experimental tiles at Station 1 only. It was present in small numbers throughout June, absent until the last week in July, whence it became quite abundant through the first week in September. Owing to the fact that it was impossible to determine the boundaries of the colonies, the terms "numbers" and "abundance" are relative and refer to the area of the tiles inhabited. Colonies were found on the tiles at all depth levels; however, they were best developed on tiles nearest the low tide level and on the 135° and 180° surfaces. Silting of these surfaces seems to be no hindrance to *P. cernua* because of its habit of continuous bowing and swaying which appears to prevent its being covered.

During preliminary experiments in October and November of 1953, glass slides which were immersed for a month under the Duke pier accumulated numerous large colonies of *P. cernua*. Therefore it is concluded that the species reproduces at least until early November.

Barentsia laxa Kirkpatrick

Considering the data accumulated from all 3 stations *Barentsia laxa* settled on the experimental tiles from the last week in July through the first week in October, with the exception of a 2-week period in mid-September. Rather sporadic settling occurred at Stations 2 and 3 as is shown in Figure 10. In terms of abundance, high counts were recorded in July and August with the most colonies developing at Station 1 and least at Station 2. The colonies were fairly evenly distributed at all depths, though there was some slight tendency toward concentration on the deepest tiles. Surfaces which were oriented at 135° and 180° supported practically all of the colonies.

Rogick (1948) noted that *B. laxa* reproduced in the Woods Hole area from the last week in July to the first week in September and suggested that the reproductive period very likely should extend on either side of these dates. This proved to be the case, at least at Beaufort, since reproduction continued into October.

Alcyonidium polyoum (Hassall)

This species is represented by only 2 colonies which appeared on the tiles at Stations 1 and 3 during the interval of May 24 to June 9. Hence it is not possible to make any estimate of the extent of the reproductive season.

Nolella stipata Gosse

Evidence from the piling studies indicates that the reproductive period in the Beaufort area for this species is at least from the last week in July to the first of October. Supplementary data from dredge and trawl collections reveal that the species reproduces as early as June 23. Settling occurred at all 3 stations, though it was discontinuous during the dates mentioned above, and was most frequent at Station 1 and least at Station 2. No surface orientation or depth concentration was noted.

Anguinella palmata van Beneden

Only 4 colonies were collected from the experimental tiles. These were recorded from a 45° surface at a depth of 6 feet at Station 3 for a 2-week period ending October 9, 1954. Glass slides suspended in the water under the Duke pier for one month terminating on November 8, 1953, supported a luxuriant growth of the species. McDougall reported *A. palmata* settling continuously on tiles at the Duke pier from August 26, 1941 (first appearance in the area), to February, 1942, with peak settlement estimated to be during October.

Collections made over a 2-year period during

the present study indicate that, contrary to McDougall's findings, the species is present all year round.

Bowerbankia gracilis Leidy

The species first appeared on the tiles in mid-June at Station 3. It was not noted again until large colonies spread over the tiles at Stations 1 and 3 from late August to November. The species was more abundant at the latter station; however, the largest number of colonies appeared at both stations during early September. No particular surfaces or depths were more favorable than others.

It is noteworthy that *B. gracilis,* which is commonly found epizoic on hydroids and other sessile invertebrates, appeared in greatest abundance during times of exceptionally heavy settling of *Pennaria tiarella, Tubularia crocea* (just beginning to appear), *Eudendrium carneum,* and *Perophora viridis.*

Aetea anguina (Linnaeus)

Aetea anguina reproduces in the Beaufort area from mid-April to early November. Its absence from the tiles during an interval of a month and a half in August and September suggests the possibility of two reproductive periods. Heaviest settling occurred in June and July with highest counts recorded for Station 3; Stations 2 and 1 followed in that order with decreasing counts.

With very few exceptions larval settlement occurred at mid-depths and increased toward the bottom. In all cases the deepest set of tiles supported a markedly higher number of colonies. Colonies became established predominantly on surfaces oriented at 0° and 45°.

The species is known to be stenohaline, requiring higher salinities, which perhaps accounts for its paucity at Station 1.

Membranipora tenuis Desor

Colonies of *Membranipora tenuis* became established on the tiles in late April and continued to appear into early December. Approximately the same counts were recorded for all 3 stations. Heaviest settling occurred from June to early August. No depth or surface selection was observed. Pomerat and Reiner (1942) found that this species had a noticeable tendency to settle on 0° and 45° surfaces at Pensacola.

Electra crustulenta (Pallas)

Evidence from the piling studies indicates that this species reproduces from March to early October. Except for one record in early June at Station 3, settlement occurred only at Station 1. This is to be expected since the species is commonly known to inhabit brackish areas.

With only two exceptions on 90° surfaces, colonies became established on 0° and 45° surfaces. Settling increased with depth.

Heaviest settlement occurred in March. Osburn (1944) reports that *E. crustulenta* reproduces in great abundance throughout the summer until late in September in the Chesapeake Bay. At Daytona Beach, Richards and Clapp (1944) reported that it first appears in March, becomes numerous in April and May, absent during the summer, abundant again in September, declines during October to absence by November.

Electra hastingsae Marcus

A single colony was found on the tiles; it was recorded April 16, 1955, at Station 2 on the undersurface of the deepest tile. It was found by Pomerat and Reiner (1942) on 0° and 45° surfaces.

Bugula turrita (Desor)

Bugula turrita was found on the tiles at Stations 1 and 3 for only 2 weeks during the last of April, 1955. Rogick and Croasdale (1949) report the collection of colonies with ovicells from the end of June through mid-August at Woods Hole. The earlier beginning of the reproductive period at Beaufort is probably to be expected.

Bugula californica Robertson

This species, new to the Atlantic coast of North America (Maturo 1957), reproduces at Beaufort from April to early December. It settled on the tiles at all 3 stations; however, Station 1 was the best site, with Stations 3 and 2 following in that order. Colonies appeared in greatest abundance during early September and December of 1954 and late April, 1955.

Larval settlement took place from the surface to mid-depths where maximum settling occurred, then decreased rather abruptly toward the bottom. But for a negligible number settling elsewhere, all colonies became established on 0° and 45° surfaces.

Some sidelights of the piling studies are perhaps worth mentioning. On the evening of November 21, 1954, zoaria which had been collected from the sides of the piling from Station 1 were placed in a finger bowl in the laboratory. The following morning, after finding a number of larvae swimming about in the bowl, a light source was placed beside the bowl so that light passed from one side to the other. The larvae were observed to swim mostly in the side of the bowl away from the light source. They swam in ro-

tating spirals, usually in contact with the side or bottom of the bowl. By mid-afternoon none was swimming. The next morning about 12 metamorphosing larvae were found attached on the side of the bowl opposite the light source and just below the waterline. Some were attached near the bottom. Late evening on that same day some ancestrulae with extended tentacles were noted. These observations compare favorably with the responses of *B. flabellata* and *B. turrita* as studied by Grave (1930) and Lynch (1949).

An ancestrula of *B. californica* which had apparently developed from an overwintering colony on a tile kept in the laboratory water table was observed in early March. Within 2 weeks 12 new zooecia had developed. A fortnight later there were about 120 zooecia.

The habit of selecting light-protected areas for attachment is further exemplified by the observation that a great abundance of *B. californica* colonies was found throughout the year in the settling tank for the saltwater system in the attic of one of the research buildings of the Duke Marine Laboratory.

Schizoporella cornuta (Gabb and Horn)

This species, which is very similar to *S. unicornis* in its early stages, was probably confused with it at the beginning of the present study. However, the reproductive period in the Beaufort area is at least from June to late October, although colonies were absent from the tiles for a period from the second week of August to the last week of September, 1954. Settlement of larvae occurred in approximately the same abundance at Stations 1 and 3 only. In practically all cases the upper limit of colony establishment was 2 feet from the bottom. With the exception of a few records for 90° surfaces, settlement occurred on 0° and 45° surfaces.

Hippodiplosia americana (Verrill)

The species is represented on the tiles by only 3 colonies, one of which was found October 9, 1954, and the others on April 17, 1955. Station 2 had no record of the species, but colonies dredged from Bogue Sound not far from the station on January 10 and July 8, 1955, had maturing ovicells. From the limited data at hand it is not possible to estimate the extent of the reproductive season.

Microporella ciliata (Pallas)

Microporella ciliata reproduces in the Beaufort area from at least late April to late October. Larvae settled on the tiles at Station 3 through this time and intermittently at Stations 1 and 2. Colonies became established only on tiles within 2 feet of the bottom, the greatest concentration being found on the lowest set of tiles (particularly the bottom-most one) and on 0° and 45° surfaces. The highest counts were recorded for late July.

Parasmittina trispinosa (Johnston)

Larvae settled on the tiles at all 3 stations from late May to late November. Two marked periods of heavy settlement were noted, one in mid-June and the other in early October. With very few exceptions, larvae settled on tiles within the range of 2 feet from the bottom, the lowest tiles being the most colonized. Surfaces oriented at 0°, 45°, and 90° supported practically all of the colonies.

Cryptosula pallasiana (Moll)

After beginning to settle in late April larvae of this species rapidly increased in numbers until early June. Following this "peak" the numbers declined until absent from the tiles by the last of July. Thereafter a few colonies became established in mid-October and early December.

The species reproduces from June to September at Woods Hole (Rogick and Croasdale 1949). Hence it might be expected that it would have a longer reproductive period at Beaufort. Richards and Clapp (1944) found it present in abundance at Daytona Beach from September to November, although they report a few present in March and April.

Settling occurred at mid-depths and below, with a tendency to increase toward the bottom. The larvae attached in all cases to 0°, 45°, and 90° surfaces.

Discussion

The occurrence of a temperature threshold for reproductive maturity has been observed for many animals. It is interesting to note that the second or fall peak of *Bugula neritina* settling at Stations 1 and 2 occurs at a time when the average air and water temperatures drop to about 15° C, and that this is the temperature to which the water and air warm up when settling first begins in the spring. Coe (1932), in seasonal studies at La Jolla, California, found that *B. neritina* settled on all experimental blocks from April to October or November. The temperature at the first appearance of the species in April was about 16° C. Colonies were rapidly establishing in May at an average water temperature of 17° C; they were sexually mature in June (18° C), and the height of reproduction occurred in July (20° C). There is close agreement with the events at Beaufort; the more rapid warming of the water here probably accounts for the month difference in reproductive

peaks. At Miami, Weiss (1948) found *B. neritina* to reproduce in the winter, attaching only after the water temperature has dropped to about 23° C. In addition to the above studies, the reports of Richards (1943), Miyazaki (1938), McDougall (1943), Richards and Clapp (1944), Whedon (1937, 1943), Edmondson and Ingram (1939), and Saito (1931) have been graphically compared by the Woods Hole Oceanographic Institution (1952), and it can readily be seen that the temperature range of 15-18° C is a reproductive threshold for the species. In the southern hemisphere Allen and Wood (1950) found peak settlement during November through January; the temperature at these times corresponded to those at peak settlement in the northern hemisphere.

Although the settling rates of *Schizoporella unicornis* show the same bimodal settling curve that McDougall obtained, there is not as close correlation of peaks with the 2 seasons of the year when the mean water temperature was approximately 22° to 25° C as he found. Richards and Clapp (1944) reported peaks for the species from about April to July and September to November at Daytona Beach. The water temperature there ranges 20° to 27° C from April through November. Edmundson and Ingram (1939) found *S. unicornis* present throughout the year in Hawaii, the annual water temperature range being about 22° to 25° C. There were apparently no obvious peaks.

It has been shown that there is a gradient in the number of bryozoans settling on the experimental tiles from the greatest at Station 1 to least at Station 2, with Station 3 being intermediate between the others. The classical environmental factors such as temperature, salinity, and light penetration do not show important differences to account for such great settling differences. Casual observation of the 3 stations would lead one to expect the reversed gradient. Lynch (1947), in his study of the larval behavior of *Bugula neritina* at Beaufort, noted that, since this species grew abundantly near the laboratory on Pivers Island on rafts and pilings within an arm's length of the surface, it was surprising to find a much altered situation less than a mile up the mouth of the Newport River. He states that here Bryozoa could not be found at all on pilings. A few sparsely growing colonies were found near the bottom of submerged objects that could be raised to the surface from a depth of 6 or 8 feet. The same situation in the Newport River was found in the present study, not only in the case of *Bugula neritina*, but for nearly all other bryozoans as well. Yet the experimental piling study showed a much larger number of bryozoan larvae settling on tiles in this area. It appears that conditions in the river are suitable for larval settling and metamorphis but are not favorable for development to maturity. The data suggest that there is either a greater population of larvae present in the river and/or that the environmental factors there are such that more larvae are able to settle and metamorphose successfully. Evidence seems to indicate that the first is not true, because a larger parent population is implied and this is contrary to observation.

The data on the current velocities seem to offer a more promising solution, for the current gradient along the three stations is inversely proportional to the settling gradient. It was found that the maximum current observed at Station 1 was 0.7 feet per second (0.4 knots) and that there were long periods of time during the tidal cycle in which there was practically no current. At Station 3 the water was in rather constant movement with a maximum speed of about 1 foot per second (0.6 knots) although occasional rates of 1.5 feet per second might be reached. Station 2 recorded the highest velocities, these being at a maximum of 3.2 feet per second (1.9 knots). These high rates were maintained for most of the tidal cycle except for the brief slack water periods. Doochin and Smith (1951), in studying the relation of water current velocities to marine boring and fouling, found that maximum growth of *Schizoporella unicornis* was reached in currents of 0.2 knots and that attachment was prevented at 1.4 knots. McDougall also found that *Bugula neritina* larvae settled in greatest abundance in the chamber of his current box which contained relatively still water.

What happens to the great number of new colonies which become established on the tiles in Newport River? Apparently the bryozoans are among the first organisms to colonize a suitable barren surface in this area, as was shown by Scheer (1945) for another locality. Perhaps when additional organisms such as hydroids begin to settle and grow larger, sediment accumulates along with the increased crowding so that the bryozoans are smothered and are no longer a major part of the fouling fauna here. Additional factors such as adult tolerances to salinity changes, available food supply and pollution probably play important roles, too. This is in keeping with McDougall's findings. Further experiments are necessary to bring more light on the solution to this problem.

Current velocities in the sound are apparently

too great most of the time to permit successful establishment of *Bugula neritina* and some other species on the tiles. However, a large number of the encrusting species may be found on shells dredged from Bogue Sound. Until conditions, including microhabitat conditions and larval behavior, are known in greater detail in such areas it is not possible to arrive at a satisfactory solution to the problem.

The over-all seasonal settling results substantiate McDougall's findings, where applicable, except for differences in relative numbers and slight differences in the time of year. These can be attributed to diffrent experimental procedures and to yearly variations in environmental conditions.

It was noted previously that marked changes (drops) in salinity at Station 1 were reflected in the vertical distribution of *Bugula neritina* on the tiles. During these periods few *Bugula* larvae settled near the surface, the numbers tending to increase rapidly toward the bottom. Lynch (1947) found that either an increase or decrease in salinity would increase the geopositive reaction of *Bugula neritina* larvae, even though the length of the natatory period was altered. The increase in the geopositive reaction of the larvae under laboratory conditions is substantiated by the observation of what is apparently the same reaction in nature at Station 1.

The success of the present study in having 19 species of bryozoans settle on the tiles is attributed to the tile orientation plan employed at each depth interval on the experimental pilings. With the exception of the 2 entoprocts and *Membranipora tenuis,* all species which settled in any abundance were found most frequently on 0° and 45° surfaces. Pomerat and Reiner (1942) also found these surfaces the best fouling accumulators with more than 90% of all bryozoans settling on them. McDougall found a similar gradient in his gravity box experiment. Silting of the 135° and 180° surfaces undoubtedly plays an important part in preventing the attachment of larvae. Doochin and Smith (1951), Fuller (1946), and McDougall have suggested the importance of this factor.

With the exception of *Cryptosula pallasiana* and *Electra crustulenta,* all of the species which settled on the experimental tiles have a wide geographical distribution or are known on our coast from New England to Brazil. The general reproductive season for these species at Beaufort is from May to November. Beaufort is near the southern limit on the Atlantic coast for the 2 exceptions mentioned, and it is noted that they do not reproduce during the summer here.

Summary

Using special pilings set with brick tile collecting surfaces, experiments were conducted in an effort to determine the reproductive periods and larval settling rates, vertical distribution, and substrate orientation preference of estuarine bryozoans in 3 localities around Beaufort, North Carolina. Data on environmental factors were collected concurrently. Of the 19 species which settled on the tiles, *Bugula neritina* and *Schizoporella unicornis* occurred in greatest abundance and are discussed in detail.

Bryozoan reproduction generally takes place from May to November in the Beaufort area.

In nearly all cases the bryozoans settled primarily on 0° and 45° surfaces. As the substrate angle increased, settling decreased. Silting of the 135° and 180° surfaces seemed to be the major factor in preventing establishment. Encrusting species were found mostly on the deepest set of tiles.

Few Bryozoa could be collected in Newport River, yet the greatest larval settling on experimental tiles occurred there. Thus a settling gradient was found in which the greatest number of colonies became established on tiles in the Newport River and the least in Bogue Sound; an intermediate condition was found in Beaufort harbor. The settling gradient seemed to be correlated with a current velocity gradient in such a manner that the lower the velocity, the greater the settling.

It is suggested that as other fouling organisms such as hydroids begin to colonize suitable barren surfaces in Newport River a greater amount of sediment accumulates along with increased crowding in that locality so that the bryozoans are smothered and are unable to become a major part of the fouling fauna there.

References

Allen, F. E., and J. E. F. Wood. 1950. Investigations on underwater fouling: II—The biology of fouling in Australia. Austral. Jour. Mar. Freshw. Res., **1**: 92-105.

Coe, W. R. 1932. Season of attachment and rate of growth of sedentary marine organisms at the pier of the Scripps Institution of Oceanography, La Jolla, Cal. Bull. Scripps Inst. Oceanogr. Univ. Calif. Tech. Ser., **3**: 37-86.

Doochin, H., and F. G. W. Smith. 1951. Marine boring and fouling in relation to velocity of water currents. Bull. Marine Sci. Gulf and Caribbean, **1**: 196-208.

Edmundson, C. H., and W. M. Ingram. 1939. Fouling organisms in Hawaii. Bernice P. Bishop Mus. Occas. Pap., **14**: 251-300.

Fuller, J. L. 1946. Season of attachment and growth

of sedentary marine organisms at Lamoine, Maine. Ecology **27**: 150-158.

Grave, B. H. 1930. The natural history of *Bugula flabellata* at Woods Hole, Mass., including the behavior and attachment of the larva. Jour. Morph. Physiol., **49**: 355-384.

Gutsell, J. S. 1930. Natural history of the bay scallop. Bull. U. S. Bur. Fish., **46**: 569-632.

Lynch, W. F. 1947. The behavior and metamorphosis of the larvae of *Bugula neritana:* Experimental modifications of the length of the free-swimming period and the responses of the larvae to light and gravity. Biol. Bull., **92**: 115-150.

———. 1949. Modification of the responses of two species of *Bugula* larvae from Woods Hole to light and gravity: Ecological aspects of the behavior of *Bugula* larvae. Biol. Bull., **97**: 302-310.

Maturo, F. J. S. Jr. 1957. A study of the Bryozoa of Beaufort, North Carolina, and vicinity. Jour. Elisha Mitchell Sci. Soc., **73**: 11-68.

McDougall, K. D. 1943. Sessile marine invertebrates at Beaufort, North Carolina. Ecol. Monogr., **13**: 321-374.

Miyazaki, I. 1938. On fouling organisms in the oyster farm. Bull. Jap. Soc. Sci. Fisheries, **6**: 223-232.

Osburn, R. C. 1944. A survey of the Bryozoa of Chesapeake Bay. Maryland Dept. Res. and Educ. Publ., **63**: 1-59.

Pomerat, C. M., and E. R. Reiner. 1942. The influence of surface angle and of light on the attachment of barnacles and other sedentary organisms. Biol. Bull., **82**: 14-25.

——, **and C. M. Weiss.** 1946. The influence of texture and composition of surface on the attachment of sedentary marine organisms. Biol. Bull., **91**: 57-65.

Richards, B. R. 1943. A study of the marine borers and fouling organisms at Wilmington, N. C. Lab. Bull. **12**: 28. William F. Clapp Lab., Duxbury, Mass. (Unpublished.)

———, **and W. F. Clapp.** 1944. A preliminary report on the fouling characteristics of Ponce de Leon Tidal Inlet, Daytona Beach, Florida. Jour. Mar. Res., **5**: 189-195.

Rogick, Mary D. 1948. Studies on marine Bryozoa. II. *Barentsia laxa* Kirkpatrick 1890. Biol. Bull., **94**: 128-142.

———, **and Hannah Croasdale.** 1949. Studies on marine Bryozoa. III. Woods Hole region Bryozoa associated with algae. Biol. Bull., **96**: 32-69.

Saito, T. 1931. Researches in fouling organisms of the ship's bottom. Zosen Kiokai (Jour. Jap. Soc. Naval Arch.) **47**: 13-64. (In Japanese; official translation on file Woods Hole Oceanographic Institution.)

Scheer, B. T. 1945. The development of marine fouling communities. Biol. Bull., **89**: 103-112.

United States Department of Commerce, Weather Bureau. 1954. Climatological data, North Carolina, **59**: 198-208.

———. 1955. Climatological data, North Carolina, **60**: 1-78.

Visscher, J. P. 1927. Nature and extent of fouling of ships' bottoms. Bull. U. S. Bur. Fish., **43**: 193-252.

Weiss, C. M. 1948. The seasonal occurrence of sedentary marine organisms in Biscayne Bay, Florida. Ecology **29**: 153-172.

Whedon, W. F. 1937. Investigations pertaining to the fouling of ships' bottoms. Biological Laboratory, Naval Fuel Depot, San Diego, Calif., Semi-annual Report for 1937-1938, December, 1937. (Unpublished.)

———. 1943. Seasonal incidence of fouling at San Diego, Biological Laboratory, Naval Fuel Depot, San Diego, Calif., Annual Report for 1942-1943.

Woods Hole Oceanographic Institution. 1952. Marine fouling and its prevention. Contribution No. 580. Prepared for Bureau of Ships, Navy Department. U. S. Naval Institute, Annapolis, Maryland.

TEMPERATURE RESPONSES AND ECOLOGICAL RELATIONS OF TWO BORNEAN LIZARDS

ROBERT F. INGER
Division of Amphibians and Reptiles, Chicago Natural History Museum

INTRODUCTION

Within the last two decades, thermoregulation in the so-called "cold-blooded" vertebrates, particularly reptiles, has attracted considerable attention. Some work has been carried on in laboratories, but a great deal has also been done in the field, where the behavioral control of temperature and the role of thermoregulation in the general ecology and evolution of reptiles are more readily apprehended (see Bogert 1949 for a review). One of the outstanding discoveries of the studies reviewed by Bogert is that reptiles regulate their body temperatures to a surprising degree by movements in and out of various portions of their habitats and by the periodicity of their activities. Other conclusions of these studies are that specific differences in preferred (or eccritic) body temperatures lead to ecological isolation and that the eccritic body temperatures of individual genera are characteristics evolved early in the history of each.

Most, if not all, of the studies of reptilian temperature responses have been conducted in the temperate zone or in the subtropics. As examples, Scortecci (1940) made some observations in North Africa, Bogert (1949, 1949a) in North America between 14° and 33° north latitude, and Fitch (1956) in central United States. These

climates are characterized by wide daily and seasonal variations that elicit cyclic behavior in reptiles partly because of their lack of endothermic mechanisms. In regions of tropical rain forest—such as the area of the present study—seasonal variation in weather is at a minimum and within the forest daily variations are damped.

To the best of my knowledge, no investigation of thermoregulation in reptiles has been conducted in the tropics. If, as seems likely, the center of poikilotherm evolution is and has been located in the tropics (Darlington 1948), it is important to have hypotheses that are now based on the temperate zone confirmed by observations in the tropics. It is for this reason that the reults of this study are presented even though they do not differ significantly from Bogert's conclusions.

Work in the field was greatly facilitated by various departments of the Colony of North Borneo for which I am very grateful. I am also indebted to the United Timbers, Ltd., and to the Bombay Burmah Trading Company, Ltd., for permission to work in their leases and for tremendous amounts of assistance. The field work would have been far less enjoyable without the many kindnesses of Messrs. P. K. Chin, O. C. Finch, Paul Isely, and John Shelley. I am grateful to Mr. C. M. Bogert for his critical reading of the manuscript. Mr. Henry S. Dybas, Chicago Natural History Museum, checked most of the identifications of food organisms.

Materials and Methods

This study concerns 2 skinks, *Sphenomorphus sabanus* and *Mabuya rudis,* the former slender and relatively small (adults 40 to 60 mm snout to vent), and the latter medium-sized (adults 80 to 95 mm) and stocky. The two skinks are easily distinguished in the field at any distance from which they can be seen so that sight records are reliable. Even juvenile *Mabuya* are noticeably stockier than *Sphenomorphus* and, besides, have a bright yellowish stripe on the neck. Adult *Mabuya* are chocolate brown above and darker on the sides. Females retain the juvenile neck stripe, whereas males acquire bright pinkish-orange or blue coloration on the chin and throat. At all ages *Sphenomorphus* appears uniform dark grayish brown. Males usually have an orange flush on each side.

Both *Mabuya* and *Sphenomorphus* are active, conspicuous, diurnal inhabitants of the floor stratum, occasionally climbing fallen timber or erect tree buttresses but rarely, if ever, higher than 2 meters. When disturbed both species, whether on a tree buttress or on the ground, seek refuge under logs, under other ground debris, or in the numerous small holes to be found in the soil at the base of every tree. If, after a *Mabuya* has been frightened into shelter, the observer remains quiet, the animal usually reappears in about 5 minutes and will continue its previous activities of foraging or basking even though the observer is in full view only 5 to 10 meters away. A *Sphenomorphus* is less likely to be seen after taking refuge, but the small size of the animal and its generally darker habitat may be as responsible as any activity of the lizard for this apparent difference. Evidently the same type of shelter is used during the night. On 2 occasions *Mabuya* were discovered at night under low mats of tangled roots against embankments.

Sphenomorphus sabanus is confined to Borneo and, since it is known with certainty only from the northeastern part of that large island, its range may be quite restricted. It is closely related to *S. variegatus* (Peters) of the southern Philippine Islands. *Mabuya rudis* may occur on Sumatra and Celebes but its known range is Borneo.

Work on these lizards was carried out as part of broader programs in the course of 2 expeditions to North Borneo in 1950 and in 1956. In 1950 work directly related to this problem was confined to observations of periods of activity and general habits and to collecting. In 1956 an irregular amount of field time was set aside for this study every week, and, although some information was obtained in the course of generalized collecting, most of the temperature data were accumulated during intervals specifically devoted to this purpose. The sun rose shortly after 06:00 hours and observation in sites inhabited by the lizards began about 06:45. Usually observation was continuous until 11:00 hours. After noon the work was more sporadic.

Notes on weather conditions, habitat, and behavior of the lizards were recorded. In some instances the lizards were watched and no attempt made to capture them. All of those collected were shot either with .22 dust shot fired from a smooth-bore pistol or with .32 dust shot fired from a 20-gauge shot-gun fitted with an adapter barrel.

All temperatures directly concerned with the lizards were obtained by means of Schulteis quick recording thermometers (described by Bogert 1949) graduated in 0.2°C. Lizard temperatures were recorded within seconds after the animals had been shot by inserting the entire bulb of the thermometer into cloacas. To avoid affecting the lizards' temperatures, each was held by a hind leg and, when in the open, in the shade of the observer's body while the thermometer was manipulated and read. Air temperatures were shaded

temperatures one-half meter above ground at the spot where each lizard was seen or shot. The temperature of the substrate was obtained by holding the bulb of the thermometer against the log, if that were the substrate, or by thrusting the bulb into the soil.

The lizards were preserved within 4 hours of capture in a 3% solution of formalin and remained in formalin for 4 to 5 months after which they were transferred to 70% ethyl aclohol in the Chicago laboratory. After transfer the stomachs were removed and the length and sex of every animal recorded. Entire food organisms were measured by means of dial calipers to the nearest 0.5 mm; lengths of food animals with part of the body missing were estimated. Identification of the food usually was carried to the ordinal level only.

As part of the general field work, camp air temperatures were recorded at 3-hour intervals beginning at 06:00 hours and ending at 21:00 hours. A Taylor Instrument Company wet-dry bulb mercury thermometer was used for this purpose and both readings recorded. These were supplemented by records of a mercury-filled, maximum-minimum thermometer. A Bristol Company thermohumidigraph, which inked a continuous record of temperature and relative humidity, was set in the forest 2 meters above the ground after being calibrated against the wet-dry bulb thermometer and a sling psychrometer. At Deramakot (see below) the thermohumidigraph was left in this position for 3 days then placed 15-17 meters above ground directly over its original position. At Kalabakan (see below), the thermohumidigraph was hung in the forest 2 meters above ground for 7 days but, because in the meantime the humidity recording arm had been damaged, only temperature was recorded. Although these instruments have Fahrenheit scales, the field records have been converted to Centigrade for the purposes of this paper.

Description of Area

The whole island of Borneo was covered by forest, tropical rain forest in the lowlands and cloud forest at high elevations, prior to settlement by man. Now the coastal fringe and strips into the interior along the major rivers are under cultivation, or are occupied by commercial centers, or were once under cultivation and then abandoned. The eastern half of North Borneo, the field locale of this study, is still largely untouched. Low-level airplane flights crisscrossing this region reveal essentially continuous primary rain forest with its characteristic undulating but unbroken canopy.

Inland from a 10- to 20-mile coastal belt, the forest is interrupted only by the major rivers and their roughly half-mile flanks of secondary growth. These distinctive bands of regenerating vegetation reflect for the most part abandoned cultivations or logging operations. Interior villages are small and widely separated until, oddly enough, the central mountain ranges are reached. But in the lowland, eastern half of North Borneo the human population of the interior is concentrated in lumber camps or in a few copra plantations. In the course of a 5-day trip covering 300 river kilometers of the Kinabatangan River, the largest river in North Borneo, I saw fewer than 200 people living outside of these major commercial camps.

Observations reported here were made at 2 principal field bases. The first of these was in the Kinabatangan basin at the confluence of the Deramakot and Kinabatangan Rivers, at the time, the site of a newly opened lumber camp. The Kinabatangan basin is low-lying and relatively flat and the Deramakot Camp, although about 300 river kilometers from the sea, is estimated to be less than 30 meters above sea level. This flat land, away from the banks of the Kinabatangan, bears a rain forest rich in vines and undergrowth.[1] The floor has a heavy layer of dead leaves and other plant debris.

At the time of my stay there (April 24—May 17, 1956), only one wide trail, varying in width from 4 to 10 meters, ran through the forest. The canopy above this strip had been cut and removed so that for most of the day the sun shone on the floor of the trail. As the trail was cut, the brush was piled at the edges (Figure 1). All other trails through the forest were at most one meter wide and were completely roofed over by the forest canopy. The great majority of *Mabuya* were seen along the wide trail that provided them with both open sunny areas and a tangled brush retreat. *Sphenomorphus,* too, were abundant along the wide trail but were also seen in numbers throughout the forest. The camp headquarters were in a cleared area, approximately 200 by 300 meters, on the bank of the Kinabatangan.

The second major field base was established on the Kalabakan River farther south and closer to the coast. In this corner of Borneo a series of low to moderately high, sharp ridges makes the topography rough. The only flat land in the Kalabakan drainage is the narrow flood plain along the river and even that is intersected by ridges running to the water's edge. Logging operations have been extensive in this basin, but, where they have not penetrated, well developed rain forest exists. The forest on these well-drained

[1] Detailed accounts of the Bornean rain forests are given by Richards (1952) and Browne (1955).

FIG. 1. Wide trail through virgin rain forest at Deramakot, North Borneo.

ridges has less undergrowth and fewer vines than the swamp forest of the Kinabatangan although the 2 forests are essentially identical in compactness of the canopy, internal stratification, and density of large trees.

The logging operations of the Kalabakan basin began about 1950 and are continuing. Mechanized means of extraction are employed with the result that damage to non-commercial timber is extensive. In a logged area virtually all of the large trees have been removed so that no semblance of a canopy remains. A few tall *Koompassia*, a leguminous species exceeding a height of 70 meters, are left standing as well as some trees of moderate height (*ca.* 25-30 meters), but these are well scattered. Dead timber and large branches that have been removed from logs are distributed through such an area. Leafy creepers are everywhere and climb over the young trees and grow up the trunks of the few remaining tall trees, forming an impenetrable tangle. Rough tractor roads 10 meters wide were scoured out for timber extraction and crisscross every logged area. On each side of such a road a 10-meter swath was cleared, but almost immediately these strips develop a low secondary growth in which wild bananas are conspicuous.

Mabuya were abundant along the roads in logged areas but not a single *Sphenomorphus* was seen even in those scattered places in which a cluster of moderate-sized trees formed a patch of dense shade. On the other hand, *Sphenomorphus* was common in the uncut forests.

Camp headquarters were in a clearing 50 by 200 meters at the edge of a logged area on the Kalabakan River and across the river from primary rain forest. This base was occupied June 1-29, 1956.

Some additional information on these skinks was obtained July 13-18, 1950, at the Sapagaya Forest Reserve near Sandakan Harbour. The relief at Sapagaya, which is close to sea level, is intermediate—not so flat as at Deramakot and not so rugged as at Kalabakan. The Reserve had been logged in 1938, but many mature trees had not been cut so that an interrupted high canopy remained or had developed in the intervening 12 years. Except for the camp clearing, no portion of this logged forest was so open as the logged areas at Kalabakan. Virgin forest surrounds the Sapagaya Reserve so that the fauna, if it was adversely affected by the timber operations, can be recruited from adjacent primary rain forest.

Both *Mabuya* and *Sphenomorphus* were seen along a wide trail (approximately 5-10 meters). This trail, for the most part shaded but at intervals open to the sky, was thus less open than the one at Deramakot yet not so densely shaded as forest proper (Figure 2).

FIG. 2. Wide trail through logged rain forest at Sapagaya Forest Reserve, North Borneo.

At Deramakot a dense mist blotted out the sun every morning until 08:00-08:30 hours. Towards 08:30 the mist began to thin and the sun, which was then relatively high, could be seen faintly. By 09:00 the sun usually was shining brightly unless obscured by high clouds. Air temperatures in the camp clearing had a range of 22.2°-34.4°C, which encompasses the air temperature range of the wide trail. The average daily maximum for the month was 32.3° and the average daily minimum 23.1°. Forest temperatures had a range of 21.1°-26.7° during a 3-day interval in which temperatures two meters above ground were recorded hourly. In Figure 3, in which temperature summaries are plotted, the Deramakot forest temperatures represent 3-day means for each hour; camp temperatures are 24-day means for 3-hour intervals.

The morning mist so characteristic of Deramakot was usually absent from Kalabakan. Except when the sky was cloudy, by 07:00 hours the sun struck the floor of the logged area surrounding

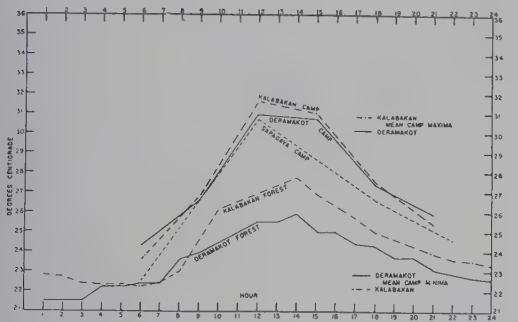


FIG. 3. Summary of air temperatures at three localities in North Borneo. See text for numbers of observations.

the camp clearing. The range of air temperatures in the camp clearing during the month of June was 21.1°-35.6°C. The mean daily maximum was 33.6° and the mean daily minimum 22.8°C. Within the forest, at 2 meters above the floor, air temperatures ranged between 21.1° and 28.9° for a 7-day period. The mean hourly forest temperatures for these seven days are plotted in Fig. 3; the camp temperatures are means for the month.

A hole in the canopy above the thermohumidigraph station at Kalabakan probably accounts for at least part of the higher temperatures of the Kalabakan forest. The sun did not shine directly on the recorder but it undoubtedly elevated the temperature in the immediately surrounding space.

Weather conditions at Sapagaya Forest Reserve were similar to those at Kalabakan. Camp air temperatures were recorded at 06:00, 12:00, 18:00, and 22:00 hours and the total range for the period of July 14-31 was 20.6°-32.2° Camp temperatures plotted in Fig. 3 are 18-day means for the four periods.

RESULTS

Food

Only 21 of the 45 *Mabuya* stomachs examined and only 22 of the 31 *Sphenomorphus* stomachs contained identifiable food organisms. The relative importance of different types of food, as determined by the number of individuals in which they occur, is approximately the same from locality to locality within lizard species. At Deramakot a higher proportion of *Mabuya* had eaten orthopterans than was true at the other localities. In *Sphenomorphus* a higher proportion of the Sapagaya specimens contained beetles, and at Kalabakan more contained miscellaneous arachnids. But these variations are quite minor and can be safely ignored.

Table I compares the occurrence of the various food categories in stomachs of the 2 lizards. Percentages under the "by stomachs" columns are calculated on the basis of the total food-containing stomachs and, as one stomach may contain more than one food type, these percentages total well over 100.

TABLE I. Occurrence of various categories of food in stomachs of two Bornean lizards

	Mabuya				*Sphenomorphus*			
	By items		By stomachs		By items		By stomachs	
	No.	%	%	No.	No.	%	%	No.
Araneida	32	*30*	*67*	14	7	*11*	*27*	6
Formicidae	0	*0*	*0*	0	7	*11*	*32*	7
Blattaria	21	*21*	*52*	11	3	*5*	*9*	2
Orthoptera	30	*28*	*71*	15	5	*8*	*23*	5
Lepidoptera	11	*10*	*14*	3	10	*16*	*32*	7
Coleoptera	2	*2*	*10*	2	14	*22*	*36*	8
Diptera	3	*3*	*10*	2	1	*2*	*5*	1
Isopoda	1	*1*	*5*	1	3	*5*	*14*	3
Arachnida misc.	0	*0*	*0*	0	4	*6*	*18*	4
Miscellany*	7	*7*	*24*	5	10	*16*	*27*	6
Total items	107				64			
Total food-containing stomachs				21				22

*Includes snails, chilopods, earthworms, and miscellaneous insect groups.

Within species, tabulation of the individual food items gives results almost identical to tabulation of occurrence by stomachs. Although the percentages vary across columns, the first 4 ranks of categories are the same in both columns.

The 4 most important food categories (Table I) in the diet of *Mabuya* are spiders, orthopterans, roaches, and lepidopteran larvae. The corresponding ranks for *Sphenomorphus* are beetles, lepidopteran larvae, ants, and spiders. These groups, with the exception of the lepidopteran larvae, are the most conspicuously abundant invertebrates on the floor stratum. However, the diets of these skinks reflect more than simple numerical availability as differences between them and certain differences between food groups can arise only as a result of selectivity. Although in the field ants appeared to be the most numerous of the 6 invertebrate groups listed above, none occurs in the *Mabuya* stomachs examined. This absence compared to the abundance of spiders and orthopterans in the same set of stomachs is not to be explained on the basis of accidents of sampling. Comparing the 2 diets, the important differences involve roaches, ants, orthopterans, and beetles. A test of the hypothesis that no difference exists between the two diets with respect to frequency of the first 6 categories of Table I yields a Chi-square value of 51.94. With 5 degrees of freedom, this corresponds to a probability of less than 0.001. Thus the difference between the 2 diets in

the 6 principal categories of food is statistically significant.

One further difference between the two lizard diets is brought out in Table I. *Mabuya* appears to be far more restrictive in its selection of food since the emphasis given 3 groups—spiders, roaches, and orthopterans—goes beyond anything comparable in the diet of *Sphenomorphus*. Considering occurrence by stomachs and ignoring the "miscellany," 3 categories appear in over half of the *Mabuya*, whereas no other food class is found in as much as one-fourth of the stomachs. On the other hand, no food class occurs in half of the *Sphenomorphus* stomachs, but 5 appear in about one-fourth or more. The same difference is evident in the "by items" columns: Three classes account for 79% of the prey of *Mabuya*, whereas even the 4 most numerous classes comprise only 60% of the organisms consumed by *Sphenomorphus*.

The size-frequency distributions of food organisms (Figure 4) have the same relationship as the taxonomic distributions. The diets of the lizards overlap extensively, in this case almost completely, yet differ in emphasis. Seventy-nine % of the food items found in the stomachs of *Mabuya* fall in size classes IV-VI (5.5-15.4 mm), whereas 73% of those in *Sphenomorphus* stomachs fall in classes II-IV (2-7.4 mm). Treating the data of Fig. 4 as a contingency table, a Chi-square value of 40.75 (P less than 0.001) is obtained indicating that the observed differences are not due to chance.

Mechanical characteristics, such as hardness or activity, of the food organisms do not seem to account for the differences between the diets. Soft-bodied organisms (*e.g.*, lepidopteran larvae, spiders, earthworms) are found in numbers in both. Hard-shelled Coleoptera are more abundant in *Sphenomorphus* stomachs, and spiny-legged Orthoptera more so in *Mabuya*. The latter feeds mainly on active invertebrates (*e.g.*, spiders, roaches, orthopterans), yet more than 50% of the food items of *Sphenomorphus* could be called active (*e.g.*, spiders, ants, orthopterans, beetles, roaches.) The possession of noxious substances by ants may be responsible for their absence from the tomachs of *Mabuya*. If so, one must assume that *Sphenomorphus* does not react to the same chemicals. On the other hand, *Mabuya* does feed on invertebrates, such as chilopods and spiders, that have poisonous secretions.

Period of Activity

At Deramakot both *Mabuya and Sphenomorphus* were collected on the open forest trail. In fact, both species were seen on precisely the same

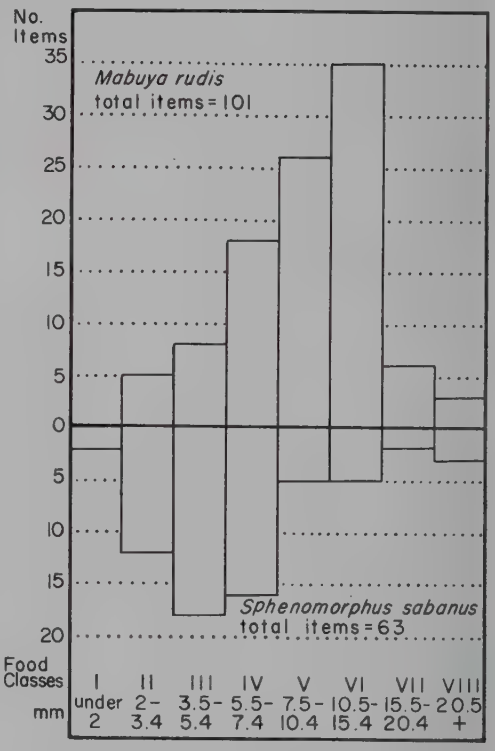


FIG. 4. Size-frequency distribution of food items eaten by *Sphenomorphus sabanus* and *Mabuya rudis*.

spot at different times. For the moment restricting consideration to observations made on the Deramakot trail, the hours of activity of the two forms scarcely overlapped (Table II). The earliest record for *Sphenomorphus* was 07:10 hours, for *Mabuya* 08:30. Except for 2 records between 15:15 and 15:45, the latest *Sphenomorphus* time was 09:01-10:00. The *Mabuya* were active much longer in the mornings, many being seen between 09:30 and 10:00; the latest time was 13:35.

As noted in a preceding section, a heavy morning mist blotted out the sun on the Deramakot forest trail until about 09:00 hours. Thus the difference between the 2 skinks in their periods of activity is closely correlated with this meterological pattern.

Along the wide trail at Sapagaya, where both species were observed, the lizards were active at different periods (Table II). The near absence of records for the early hours reflects my own activity in other parts of the Reserve at that time of day. The differences in activity agree with observations at Deramakot: *Mabuya* is more active in semi-open areas during the heat of the day and

TABLE II. Period of activity of two skinks on a forest trail at Deramakot and Sapagaya, North Borneo

Period	Number Observed	
	Mabuya	Sphenomorphus
Deramakot		
before 09:01	2	18
09:01-12:00	23	1
15:00-16:30	0	2
Sapagaya		
08:30-10:30	0	1
10:30-12:00	9	0
17:00-18:00	2	11

either seeks or remains in shelter when environmental temperatures are relatively low. On the other hand, *Sphenomorphus* is more active when environmental temperatures are low (see Fig. 3).

At Kalabakan where no morning mist obscured the sun, *Mabuya* was active in the logged areas much earlier, its time-frequency distribution there being: before 09:01-4; 09:01-12:00-8; 08:30-09:45 2.

Temperature Responses

Body temperatures of the 2 lizards and associated environmental temperatures are given in Table III. Differences between the 2 species are large and statistically significant at the 1% level. Body temperatures of *Mabuya* were higher than the corresponding air temperature with one exception, and higher than substrate (logs, leaf litter, or soil) temperatures except for 3 lizards that were cooler and 2 that did not deviate from the substrate. As Table III shows, positive deviations from environmental temperatures were great. By contrast, *Sphenomorphus* diverged very little from environmental temperatures. Only 2 individuals were cooler than the air, none cooler than the substrate, and the maximum positive deviation was only 1.8°.

The general behavior of these skinks provides explanations for the temperature differences observed. *Mabuya* often remained in the sunlight for long periods, basking or searching for food. It clearly absorbed heat faster than the air or the substrate, for in general the higher its body temperature the greater the divergence from these environmental temperatures. *Mabuya's* rapid heat absorption is also indicated by the fact that, once the floor was flooded with bright sunlight and once the lizard had moved from its nocturnal shelter into the sunlight, the time of day had little effect on body temperature or the disparity between it and environmental temperatures.

The individuals of *Mabuya* with body temperatures (respectively 25.4°, 26.0°, and 25.8°) within the temperature range of *Sphenomorphus* were shot between 09:03 and 09:15 hours in deep shade. Evidently they were just emerging from their nocturnal shelters and had not had an oppor-

TABLE III. Relation between body and environmental temperatures (°C) in two Bornean lizards

MABUYA RUDIS

Animal	Animal minus air	Animal minus substrate	Hour
25.4	− 1.8	−2.4	09:35
25.8	+ 1.4	0	09:15
26.0	+ 0.6	+0.4	09:03
28.4	+ 0.2	+2.0	09:37
28.4	+ 2.6	−0.4	08:30
29.4	+ 3.0	+2.6	09:15
29.6	+ 3.8	+2.2	08:25
29.8	+ 3.6	+2.0	09:30
30.2	+ 5.0	+3.6	07:35
31.6	+ 4.4	+3.8	09:40
31.8	+ 3.4	+3.2	09:43
31.8	+ 4.8	+2.2	11:00
32.2	+ 7.2	+2.8	10:40
32.8	+ 5.0	+2.2	09:45
33.2	+ 6.0	+3.0	10:50
33.2	+ 3.4	+1.6	11:00
33.4	+ 6.6	+4.8	09:25
33.8	+ 6.4	+5.2	09:30
33.8	+ 7.0	+5.4	09:30
34.2	+ 4.6	+0.6	10:40
34.4	+ 8.4	+7.0	10:52
34.8	+ 8.8	+6.8	10:50
35.2	+10.6	+3.6	09:20
35.6	+ 7.6	0	11:35
35.8	+ 8.8	+7.2	09:35
36.0	+ 9.6	+4.0	09:52
36.7	+ 2.5	−0.5	13:35
37.6	+ 8.0	+6.4	11:05
37.8	+10.2	+9.4	10:10
38.4	+10.2	+5.6	09:35
38.6	+ 8.4	+8.0	11:20
	Mean ± SE		
32.76 ± 0.66	+5.50 ± 0.58	+3.30 ± 0.50	

SPHENOMORPHUS SABANUS

Animal	Animal minus air	Animal minus substrate	Hour
24.0	+ 0.2	+0.2	08:15
24.6	+ 0.8	+1.0	08:30
24.8	+ 0.6	+0.2	08:55
25.2	+ 0.4	0	09:20
25.4	+ 0.2	0	09:40
25.4	+ 0.4	+0.6	07:10
25.4	+ 0.6	+0.6	08:27
25.4	+ 0.6	+0.2	08:45
25.8	+ 1.2	+0.4	08:10
26.0	+ 1.8	+0.8	07:23
26.0	− 0.2	0	09:00
26.4	+ 1.6	+1.2	08:17
26.6	+ 0.6	+0.4	07:25
26.6	+ 1.6	+1.2	08:55
26.8	− 1.7	+0.8	09:00
28.4	+ 0.6	0	15:45
	Mean ± SE		
25.80 ± 0.26	+0.58 ± 0.21	+0.47 ± 0.11	

tunity to bask. Since their body temperatures approximated the soil temperatures (25.8°, 25.6°, 25.8°) and diverged somewhat more from air temperatures (27.2°, 25.4°, 24.4°), probably their body temperatures at night were determined by the substrate temperatures of the nocturnal shelters.

Contrasting sharply with *Mabuya, Sphenomorphus* was never observed to remain stationary in sunlight. It was seen at intervals in a sunlit portion of trail at Deramakot, but on these occasions it was always at the edge of the trail and always in motion, usually moving into shelter in a very short time. If, however, the sun were obscured, *Sphenomorphus* would remain in an area open to the sky for 3 or 4 minutes.

This behavior is reflected in the approximation of *Sphenomorphus* body temperatures to the forest air temperatures. Nine of the 16 had temperatures between 24.0° and 25.8°, a temperature range found in the forests of both Deramakot and Kalabakan between the hours 09:00 to 18:00 (Fig. 3). Six additional lizards had temperatures in the range 26.0°-26.8°, the last being 0.9° higher than the maximum forest temperature at Deramakot but well within the range of the Kalabakan forest.

Deviations of *Sphenomorphus* temperatures from those of environment were usually very small (Table III), 11 of 16 differing from air temperatures by less than 1.0°C and 13 differing from the substrate by less than 1.0°C. Conceivably, positive deviations of this magnitude could be at least partially caused by the heat of the shot. If even part of the elevation in body temperatures can be eliminated because of this artificial factor, the correspondence with Deramakot forest temperatures is even closer than indicated.

Discussion and Conclusions

It is evident from preceding sections that *Mabuya* and *Sphenomorphus* have overlapping habits. Their diets, for example, include large proportions of spiders, roaches, and lepidopteran larvae, although in the sample examined *Mabuya* feeds much more heavily on orthopterans than *Sphenomorphus* and the latter consumes more beetles than does *Mabuya*. Despite the difference in the sizes of these lizards, their food items have approximately the same size range though the dominant food size classes are not identical (Fig. 4). The groups of animals on which the 2 skinks feed are so abundant that food supply is not likely to become a limiting factor. However, these skinks may still compete for food in the sense that ". . . competition occurs when the animals seeking that resource . . . harm one another in the process" (Andrewartha and Birch 1954, p. 22).

Where the habitat requirements of just one or the other lizard are satisfied, there can be no competition for food. It is only at the edge of forest and at openings within forest that food competition is at all possible. Where the habitats coincide, the lizards are likely to come in contact especially since they will be searching for similar types of prey. Contacts, which would probably be limited to visual perception, could interfere with activities such as feeding. Bilski (summarized by Allee 1931) found that the growth rate of larval *Bufo* and *Rana* decreased as the number of individuals in an aquarium increased even though the density relations were held constant by increasing the size of the aquaria. Apparently the increased frequency of contacts between individuals contributed to a retardation of growth. Bilski's experiments dealt with intraspecies groups but the results might be extended to cover interspecies groups, particularly if the species had similar habits as in the present case.

T. Park (*in* Allee, *et al.* 1949) has summarized other effects of crowding, which at its simplest level may involve just two individuals, and includes among the potential effects reduction in rates of reproduction, of learning, of respiration, and of movement in species that normally do not live in aggregations. In some cases the stimulation resulting from contact between individuals is presumed to be the actual means by which these other physiological functions are inhibited or retarded. Extending speculation still farther, it is at least conceivable that interspecies contacts might interfere with reproductive functions of the 2 Bornean skinks. In this connection it is pertinent that both *Mabuya rudis* and *Sphenomorphus sabanus* oviposit under logs and other floor debris.

Information on these skinks, however, is limited to observations brought out in preceding pages and does not include observations on interspecies contacts. Nevertheless, it is clear that such contacts are minimized by the differences in periodicity of activity. Temperature responses provide the mechanism effecting this isolation.

Mabuya rudis customarily does not become active until the sun shines brightly on the substrate, in other words, until radiant heat is sufficient to elevate its temperature 4 to 10 degrees above the usual morning air temperature. As the radiant heat diminishes in the late afternoon *Mabuya* retires. *Sphenomorphus sabanus,* however, responds in just the opposite fashion. Along open trails like those at Deramakot and Sapagaya,

its characteristic body temperatures are possible only if it confines its activity to the periods before and after the interval of intense insolation.

Differences in temperature responses also lead to habitat isolation. Since the high body temperatures of *Mabuya* are attainable only with direct insolation, this species is restricted to sunny patches of the forest floor while *Sphenomorphus* can find suitable thermal conditions throughout the forest.

Observations made one morning in the Kalabakan forest illuminate this difference between *Mabuya* and *Sphenomorphus* especially well. On that day (June 27) the sky was clear but, as usual within the forest, the sunlight penetrated to the floor only in widely scattered small patches. Two *Sphenomorphus* were shot in dense shade at 08:15-08:30 at which time the air temperature was 23.8°; animal temperatures were 24.0° and 24.6°. At 10:25-10:45 two agamid lizards (*Gonyocephalus liogaster*) were shot on the ground and in dense shade also. Their temperatures were 25.6° and 25.8°. By this time the air temperature had risen to 26.0°. Less than 20 meters away from the place where the second agamid was killed 2 mabuyas were shot in a patch of sunlight at 10:50-10:52. The temperatures of these skinks were 34.4° and 34.6° and the air temperature in adjacent shade 26.0°. Except for the presence of sunlight, the floor at this spot differed in no apparent way from the floor elsewhere in the forest. Theoretically, the floor stratum throughout the forest is available to all 3 species. But the temperature requirements of *Mabuya* confine it to those limited areas of the floor reached by sunlight (or to the immediate vicinity of such places), whereas *Sphenomorphus* and other truly forest lizards are not thus restricted.

That the high body temperatures of *Mabuya* reflect physiological requirements and not merely the effects of a particular habitat is demonstrated by its earlier daily appearance at Kalabakan, which lacked the morning mist characteristic of Deramakot. Equally high body temperatures were obtainable at Deramakot, but not at the same early hour. The fact that *Sphenomorphus* was active in open areas, such as the wide trail at Deramakot, only when the sun was low and air temperatures approximated those of the forest is evidence that its low body temperatures represent physiological necessity. As long as an open area had the thermal characteristics of the forest, it was a suitable habitat for *Sphenomorphus*. Whenever and wherever the forest had the thermal characteristics of a clearing, it became a suitable habitat for *Mabuya*.

The origins of these temperature responses probably lie far back in the phylogenies of these skinks. The genus *Mabuya* is circumtropical and most of the species, like *rudis*, are usually seen in open, sunny places. The American species *mabouya* (Dunn 1944, Schmidt 1920), the African forms *quinquetaeniata* (Schmidt 1919) and *striata* (Loveridge 1953), and the Asiatic species *dissimilis* (Smith 1935), to cite just a few, are frequently observed basking in open places.

On Borneo itself 2 additional species of *Mabuya* occur. One (*multifasciata*) is never found in forest and appears to be limited to very large clearings near the coast. Twelve *multifasciata* were collected in the Kalabakan camp clearing and these had body temperatures varying from 29.6° to 37.8° (mean = 33.65°; mean of *rudis* = 32.76°). I have made no field observations on the third Bornean species, *multicarinata;* but in the Philippines it is found only in sunny places at the edges of forests (Taylor 1922).

The association of widely separated species of *Mabuya* with basking habits in open, sunny areas and the agreement of the temperatures of *multifasciata* with those of *rudis* lead to the conclusion that the temperature responses of *rudis* are characteristic of many and possibly all species of the genus.

The species of *Sphenomorphus* do not offer so clear a picture. The genus (or subgenus, according to some authors) is found from India to Australia and, though some species live in open areas, none has been reported to bask. The species occurring in Borneo are forest inhabitants and those known from the Philippine Islands have usually been observed in or near trees (Taylor *op. cit.*). Despite the lack of definite and direct information it is very likely that the genus has a lower range of preferred body temperatures than does *Mabuya*.

Summary

The 2 Bornean lizards, *Sphenomorphus sabanus* (snout-vent 40-60 mm) and *Mabuya rudis* (80-95 mm), are diurnal inhabitants of the floor stratum. *Sphenomorphus* lives throughout the lowland rain forest and along its edges. *Mabuya,* on the other hand, is most abundant along the forest edge and in large clearings. Within the forest it is confined to areas of the floor reached by sunlight.

These lizards feed on the invertebrates common in their habitats. Although the same taxonomic groups occur in both diets, *Mabuya* feeds primarily on spiders, orthopterans, roaches and lepidopteran larvae, in that order, whereas *Sphenomorphus* feeds mostly on beetles, ants, lepidopteran larvae, and spiders. Similarly, though the size

range of the food is practically identical (1-25 mm *Sphenomorphus;* 2-32 mm *Mabuya*), 79% of the items eaten by *Mabuya* falls in the range 5.5-15.4 mm and 73% of the food of *Sphenomorphus* in the range 2.0-7.4 mm.

The periods of activity of the 2 species scarcely overlapped where their habitats coincided. Along open forest trails at 2 field bases in North Borneo, 88% of the 33 *Sphenomorphus* recorded were observed prior to 09:00 or after 17:00 hours. Eighty-eight % of 36 *Mabuya* recorded at those bases were observed between the hours of 09:00 and 17:00. Thus *Mabuya* was active during the heat of the day while the sun shone on large areas of the trails, but *Sphenomorphus* only when environmental temperatures were low.

Although the range of body temperatures recorded for *Mabuya* was 24.5°-38.6°C, only 8 individuals out of 31 had temperatures below 30°. In general, body temperatures of *Mabuya* ran 3°-10° higher than environmental temperatures, a difference that can be accounted for only by the lizard's habit of basking. Body temperatures of *Sphenomorphus* varied between 24.0° and 28.4°C, departing from environmental temperatures by less than 2°.

The failure of *Mabuya* to become active until the sun was moderately high and its habit of basking suggest that it requires elevated body temperatures for efficient activity. On the other hand, the avoidance by *Sphenomorphus* of open areas while the sun is high and its restriction to forest suggest that it operates most effectively at relatively low body temperatures. These differences tend to isolate the 2 species ecologically since the individual physiological requirements are best satisfied either by distinct habitats within the forest (clearings versus the forest generally) or by different periods of activity.

References

Allee, W. C. 1931. Animal aggregations. A study in general sociology, Chicago, University of Chicago Press.

———, **A. E. Emerson, Orlando Park, Thomas Park, and K. P. Schmidt.** 1949. Principles of Animal Ecology. Philadelphia, W. B. Saunders Company.

Andrewartha, H. G. and L. C. Birch. 1954. The distribution and abundance of animals. Chicago, University of Chicago Press.

Bogert, C. M. 1949. Thermoregulation in reptiles, a factor in evolution. Evol., 3: 195-211.

———, 1949a. Thermoregulation and eccritic body temperatures in Mexican lizards of the genus *Sceloporus.* An. Inst. Biol., 20: 415-426.

Browne, F. G. 1955. Forest trees of Sarawak and Brunei and their products. Kuching, Sarawak, Govt. Printing Office.

Darlington, P. J. 1948. The geographical distribution of cold-blooded vertebrates. Quart. Rev. Biol., 23: 1-26, 105-123.

Dunn, E. R. 1944. Los generos de anfibios y reptiles de Colombia, II. Reptiles, orden de los saurios. Caldasia, 3: 73-110.

Fitch, H. S. 1956. Temperature responses in free-living amphibians and reptiles of northeastern Kansas. Univ. Kansas Publ., Mus. Nat. Hist., 8: 417-476.

Loveridge, Arthur. 1953. Zoological results of a fifth expedition to East Africa, III. Reptiles from Nyasaland and Tete. Bull. Mus. Comp. Zool., 110: 143-322.

Richards, P. W. 1952. The tropical rain forest. Cambridge, Cambridge University Press.

Schmidt, K. P. 1919. Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909-1915. Part I. Turtles, crocodilians, lizards, and chameleons. Bull. Amer. Mus. Nat. Hist., 39: 385-624.

———. 1920. Contributions to the herpetology of Porto Rico. Ann. New York Acad. Sci., 28: 167-200.

Scortecci, Giuseppi. 1940. Biologia Sahariana. Napoli, Edizioni della Mostra d'Oltremare. (Not seen.)

Smith, M. A. 1935. The fauna of British India. Reptilia and Amphibia. Vol. II.—Sauria. London, Taylor and Francis.

Taylor, E. H. 1922. The lizards of the Philippine Islands. Bureau Sci. Manila, Publ. No. 17.

THE SEX AND AGE STRUCTURE OF ROOSTING STARLINGS

David E. Davis

Johns Hopkins University, School of Hygiene and Public Health

For a number of places and times the sex ratio of starlings (*Sturnus vulgaris*) has been reported to be in favor of males. The purpose of this paper is to analyze the age composition of a roost and to offer an explanation for the preponderance of males. Kessel (1951) reviews numerous European and American studies. In Holland 52.3% of 305 birds in one place and 57.4% of 290 in another were males (Kluijver 1935). In England 71.1% of 786 birds were males (Bullough 1942). In Ohio 68.3% of 3161 birds were males (Hicks 1934). In New York 52.7% of 455 birds were males (Stegman 1954). Only one report has less than 50% males; Loefer and Patton (1941) found that 45.3% of 285 birds were males. Although only the samples from England and from

Ohio are significantly different from 50% male, the consistency was notable. Since a differential mortality of the sexes might explain this aberration from the expected 50% male, an analysis of the age composition was begun.

Methods

The birds were collected at night from a roost in cupolas on a building of the Johns Hopkins Hospital (Davis 1956). A trap was built that captured part of the birds inside of the cupola but none of the birds that roosted outside on the ledges or in the vines. The trap was used to catch birds once or twice a week from November to March from 1952-1957. In most cases all birds were brought to the laboratory for banding or experimental work. At first (1952) so many birds were caught that not all could be used and the excess was freed.

In the laboratory each bird was banded and information obtained on bill color and sex. At the same time hackle feathers from the upper throat, the underwing coverts, and the outer tail were collected and stored. Sex was determined by the presence (females) or absence (males) of a ring in the eye and confirmed by the feathers as described by Kessel (1954). The accuracy of the eye ring test was determined by examination of the gonads of 951 birds in 1952. Only 8 of 687 birds that lacked a ring were females (1.16%) while 7 of 264 birds that had a ring were males (2.65%). This error is neglected in subsequent analysis. At later times the length of iridescence on three hackle feathers from each bird was measured to the nearest millimeter and the average was recorded. It is important to note that the white tip of the feather was excluded from this measurement. For an understanding of the aging procedure it is necessary to note that the starling lacks a spring molt of the hackle feathers. Thus the feathers that grow in September are the prenuptial molt and should be called the first, or second, *etc.* nuptial feathers.

Analysis of the frequency distribution of the lengths of the iridescence on the hackle feathers was taken directly from a paper by Cassie (1954) that describes a method for separating a polymodal frequency distribution into its components. The details of calculation are not repeated here but the chart calculated from data on male starlings is given (Figure 1). The curved line (triangles) is the cumulative percentage distribution for the males. The straight lines (dots) are the frequencies for two categories of feather lengths. From these lines, which represent normal distributions, the mean (at the 50% point) and the standard deviations (at 16% and 84%) are determined. The chart for females is similar. The proportion of the two groups of birds for each sex are obtained from these calculations. Note that while we assume from knowledge of the growth of feathers and from the work of Bullough (1942) and Kessel (1954) that the two groups (for each sex) represent adults and birds born in the preceding spring, nevertheless this analysis permits only the conclusion that there are two groups. The validity of this assumption is tested by recaptures of banded birds as described below.

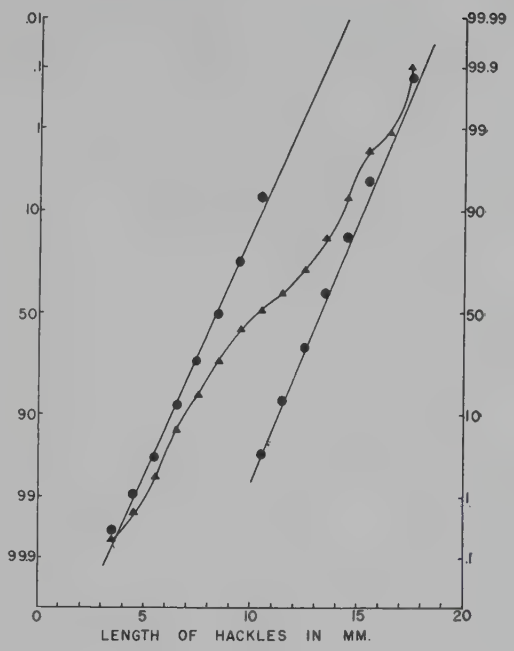


Fig. 1. The length of hackles of males showing separation into two normal distributions.

It is apparent that this technique determines how many starlings of the group have feathers in a specific length class but, for an individual bird, only the probability that it belongs to a particular class. Table I gives the means, standard deviations, range, number and percentage in each group. To determine the class of an individual requires a consideration of the overlap of the two distributions.

From an examination of the overlap area under these normal curves, we can establish arbitrary limits for individual males. (1) Throat feathers 10 mm or less (2) an intermediate group having feathers 10-12 mm and (3) feathers 12 mm and over. This intermediate group includes most of the overlap of the two distributions. There is, of course, a small percentage (1.7%) of Class A that extends past the indeterminate zone into

TABLE I. Statistics on classes of starlings captured from November to March

Class	Male		Female	
	A	B	A	B
Mean length of feathers (mm)	8.4	13.3	4.9	8.5
Two standard deviations (mm)	3.4	3.0	2.4	2.6
Mean plus 2 standard deviations (mm)	11.8	16.3	7.3	11.1
Mean minus 2 standard deviations (mm)	5.0	11.3	2.5	5.9
Number of starlings in group	604	474	564	241
Percentage (of each sex) in group	56.0	44.0	70.0	30.0

group 3 and likewise a part of Class B is found in group 1 (1.4%). These proportions are listed on Table II and are considered negligible.

TABLE II. Boundaries of measurements for individual Starlings

	Length Class		
	A less than	Indeterminate	B more than
Feather Length (mm)			
Males	10 mm	10-12 mm	12 mm
Females	6	6- 7	7
Percentage of same class excluded			
Males	17%	.....	19%
Females	18	.....	12
Percentage of other class included			
Males	1.4	.....	1.7
Females	1.8	.....	5.4

The result of these calculations is that for each sex we have three groups to which an individual may be assigned (Table II). A male with feathers less than 10 mm is almost certainly Class A; one with feathers between 10 and 12 is indeterminate; one with feathers longer than 12 mm is almost certainly Class B. The assignment of females to classes is similar (Table II). These lengths are almost the same as the standards suggested by Kessel (1954) based on 89 birds caught in the late fall.

On this basis individual birds are classed as in Table II. Now we can return to the question of the age of the two groups of birds in the population by analyzing the recaptures of banded birds. From 1952-56 birds were banded and released in each winter. Feathers were saved in all years and measured in 1956. The length class (A or indeterminate or B) when banded and when recaptured is given in Table III. It is obvious that a bird recaptured in a subsequent year must be about 17 or more months old. These data show that no bird belonged to Class B in one year and Class A in a subsequent year. We find that 14% of the birds are indeterminate. This value is close to the average of 19% and 12% derived from the curves (Table II). From these results we conclude that class A birds are subadults (7-11 months of age) and class B birds are adults (19-23 or 31-35 or 43-47, *etc.* months of age). The fact that about 30% of the subadults had indeterminate hackles suggests that a high proportion of the indeterminate birds are really 19-23 months old. The terminology and chronology are given in Table IV.

TABLE III. Classification of hackle lengths of starlings recaptured in subsequent years (males and females)

Class when banded	Class one molt after banding			Class two or more molts after banding		
	A	indet.	B	A	indet.	B
A	0	10	24	0	1	1
Indeterminate	0	1	11	0	1	8
B	0	2	49	0	0	9
		13	84		2	18

TABLE IV. The terminology and chronology of age classification used for starlings

Months	Plumage	Age in months	Name for age
May	Nestling	0	Nestling
June-Sept.	Juvenal	1- 4	Juvenile
Sept.-Sept.	First nuptial	5-16	Subadult
Sept.-Sept.	Second nuptial	17-28	Adult
Sept.-Sept.	Third nuptial	29-40	Adult

A number of problems arise in sampling the feathers. The feathers in different parts of the throat vary in length, therefore a group was pulled from the same part of the throat of each bird. Even these feathers vary and hence three feathers were measured and averaged. Obviously, it would be desirable to measure more feathers per bird but the work involved was considered excessive. There is little reason to expect a bias since the feathers were measured routinely with no knowledge of the history of the bird or of the expected age composition.

Results

Several aspects of the results have unavoidably been discussed under methods. In Table I it is seen that 56.0% of the males and 70.0% of the females are subadults. This difference is statistically significant and suggests a consideration of the hypothesis that differential mortality accounts for the high proportion of males. We can approach this hypothesis by considering the proportion of young in a population. If the population is stationary and if the recruitment and death rates are constant, then the mortality of adults is given by

the proportion of young since each young replaces an adult. If we assume a stationary population and constant birth and death rates then the probability of dying for adult males is 0.56 and for adult females is 0.70.

The first problem to consider is the age at which this calculated difference in mortality occurs. The percentage of males (calculated from data in Table I) is 57.2 for all birds, 66.3 for adults and 51.7 for subadults. Furthermore the percentage of males among the subadults in February and March is the same (51.7) as that for all winter, indicating that the presumed differential mortality between the sexes occurs after March. Since this percentage is not significantly different from the expected 50% male it is concluded that mortality is the same for both sexes during the first 10 months of life. Now an hypothetical population of 51.7 males on, say, April first will decline in successive years as follows: 22.8, 10.0, 4.4, 1.9, 0.8, 0.4, *etc.* due to a probability of surviving of 0.44. Similarly 48.3 adult females will decline: 14.5, 4.4, 1.3, 0.4, *etc.* due to a probability of 0.30. If we add up the totals of these birds we have 41.8 adult males and 20.6 adult females or 66.8% males which is statistically indistinguishable from the observed 66.3% of males in the adults in Table I.

The close agreement of the observed and hypothetical age compositions points to the conclusion that a differential mortality occurs between the sexes. It can be said that this presumed mortality occurs between March and November because in November the percentage of males is statistically indistinguishable from the percentages later in the winter.

It needs to be recognized that an alternative hypothesis, namely, that the adult females tend to roost on the vines outside the cupola, has not been excluded. Unfortunately a direct test of this hypothesis by capturing birds is not practical.

Mortality data are available for several European populations (Lack and Schifferli 1948) but both sexes are included. Birds banded as juveniles had a probability of dying of 0.52 in England (197 birds) and 0.63 in Switzerland (306 birds). The probability of dying during the first year after banding was 0.66 for 592 English birds and 0.73 for 394 Swiss birds. Beyond the first year the values are 0.55 and 0.62 respectively. It appears that the data for Baltimore (61.8% subadults, sexes combined) suggest a mortality rate closer to that in Switzerland than that in England.

Summary

From 1951-1957 starlings were trapped in winter in a roost. Data on sex and feather characteristics were used to determine that 56.0% of the males and 70.0% of the females were subadults (first year). Also 51.7% of the subadults were males and 66.3% of the adults were males. If we assume a stationary population we can use the proportion of subadults as the probability of dying and follow an imaginary population of 51.7 males and 48.3 females through successive years. The sex composition of this hypothetical population is 66.8% male which is indistinguishable from the observed percentage. This result agrees with the conclusion that the observed difference in sex composition results from an excessive mortality of females.

References

Bullough, W. S. 1942. The reproductive cycles of the British and Continental races of the starlings. Phil. Trans. Roy. Soc. London B **231**: 165-246.

Bullough, W. A. 1942. On the external morphology of the British and Continental races of starling (*Sturnus vulgaris* Linnaeus). Ibis **6**: 225-239.

Cassie, R. M. 1954. Some uses of probability paper in the analysis of size frequency distributions. Australian J. Marine and Freshwater Res. **5**: 513-522.

Davis, David E. 1955. Population changes and roosting time of starlings. Ecology **36**: 423-430.

Dunnet, George M. 1955. The breeding of the starling *Sturnus vulgaris* in relation to its food supply. Ibis **97**: 619-661.

Hicks, L. E. 1934. Individual and sexual variations in the European starling. Bird-Banding **5**: 103-118.

Kessel, Brina. 1951. Investigations on the life history and management of the European Starling (*Sturnus vulgaris vulgaris* L.) in North America. Ph.D. Thesis; Cornell.

——. 1954. Criteria for sexing and aging European Starlings (*Sturnus vulgaris*). Bird-Banding 22: 16-23.

Kluijver, H. N. 1933. Bijdrage tot de biologie en de ecologie van den spreeuw (*Sturnus v. vulgaris* L.) gedurende zjin voortplan-Wangeningen, **69**: 1-146.

Lack, David. 1948. Natural selection and family size in the starling. Evolution **2**: 95-110.

——, and **Alfred Schifferli.** 1948. Die lebensdauer des stares. Ornith. Beobachter. **45**: 107-114.

Loefer, John B. and **A. J. Patten.** 1941. Starlings at a blackbird roost. Auk **58**: 333-348.

McAtee, E. A. 1940. An experiment in songbird management. Auk **57**: 333-348.

Stegeman, Leroy C. 1954. Variation in a flock of the European Starlings. Auk **71**: 179-185.

EFFECT OF VEGETATIONAL COVER OF FENCE ROWS ON SMALL MAMMAL POPULATIONS[1]

Introduction

Extensive land cultivation in Whitman County, Washington, has reduced the natural habitats of native animals considerably. For many animal species, fence lines are one of the few habitats resembling primitive conditions which remain. These refuges have been disturbed to varying degrees. This investigation was made to obtain an indication of the differences in small mammal populations of fence rows having different vegetational cover.

Methods

The study was made in the farmlands south of Pullman. Three types of fence lines were studied: shrubby fence line, weedy fence line, and fence lines which were virtually bare of vegetation. Three transect samples were selected along each of the three types of fence lines. The basis for selection was uniformity in vegetational cover. The plant species present in each transect sample were recorded.

Twenty spring traps (mouse traps) were placed at 1 meter intervals under each fence studied. A mixture of peanut butter and oatmeal was used for bait. As a check on this trapping technique, "fall-traps" were used, consisting of a can of water sunk into the soil to ground level. One of these "fall-traps" was placed at each end of every line of spring traps. The traps were baited and set in the late afternoon and the animals were removed from them on the following morning. The trapping was done on four nights in October.

Description of the Fence Lines

The fences which were studied were constructed of barbed wire fastened to wooden posts.

All the fence lines occurred on cultivated phases of the *Festuca idahoensis/Symphoricarpos rivularis* and *Agropyron spicatum/Poa secunda* habitat types (Daubenmire 1942). The vegetation of the weedy fence lines was composed of a dense row of introduced weedy species: *Cirsium vulgare* (Savi) Airy-Shaw, *Sonchus asper* (L.) Hill, *Arctium lappa* L., *Madia glomerata* Hook., *Galium aparine* L., *Marrubium vulgare* L., *Amsinckia lycopsoides* Lehm., *Descurainia sophia* (L.) Wetts., *Sisymbrium altissimum* L., *Amaranthus graecizans* L., *Chenopodium* sp., *Avena fatua* L., *Bromus tectorum* L., *Bromus japonicus* Thunb. The shrubby fence lines were composed of very dense rows of *Rosa ultramontana* (Wats.) Heller. The bare fence lines were very narrow and had been recently burned. The vegetation consisted solely of very short, sparse grass shoots. Such plants would provide no cover for the small mammals, and afford only meagre food.

The fields on both sides of the fences had been tilled shortly before the trapping was done. The fields bordering the three weedy fence lines had been used as follows: on one side, current year's stubble which had been burned and then tilled; on the other side of the fence, summerfallow which had just been seeded to wheat. The fields of wheat stubble bordering the shrubby fence lines and the three bare fence lines had been plowed under. The fields had been tilled close to the bare fence lines and in addition the fence lines had been burned.

[1] The writers wish to acknowledge the helpful suggestions of Dr. R. F. Daubenmire and Dr. I. O. Buss.

Results

The results from four trapping nights are shown in Table I.

Table I. Results of trapping

Fence type		Weedy			Shrubby			Bare			Total for trapping night
Site number		1	2	3	4	5	6	7	8	9	
First trapping X/20/57	P.m.	0	2	1	1	6	3	2	2	5	
	M.m.	0	2	0	1	0	0	0	0	0	
	M.l.	0	0	0	1	1	0	0	0	0	
	S.v.	0	1	0	0	0	0	0	0	0	
	Total	0	5	1	3	7	3	2	2	5	28
Second trapping X/23/57	P.m.	0	2	1	4	2	2	2	2	0	
	M.m.	0	4	3	0	0	0	0	0	0	
	M.l.	0	0	0	0	1	0	0	0	0	
	S.v.	0	0	0	0	0	1	0	0	0	
	Total	0	6	4	4	3	3	2	2	0	24
Third trapping X/27/57	P.m.	4	8	3	3	4	3	4	6	4	
	M.m.	1	0	3	1	0	0	0	0	0	
	M.l.	0	0	0	0	1	0	0	0	0	
	S.v.	0	1	0	0	0	0	0	0	0	
	Total	5	9	6	4	5	3	4	6	4	46
Fourth trapping X/30/57	P.m.	7	9	8	7	8	3	7	2	6	
	M.m.	1	3	0	1	1	1	0	2	0	
	M.l.	0	0	0	0	0	0	0	0	0	
	S.v.	0	1	0	0	0	0	0	0	0	
	Total	8	13	8	8	9	4	7	4	6	67
Grand total for site		13	33	19	19	24	13	15	14	15	
Grand total for fence type				65*			56*			44*	165

*These data are shown to be not significantly different by Student's t distribution (Snedecor, 1956), at the 5% level.
Probability of a larger value of t for differences between:
(1) Weedy *vs.* Shrubby: $p > 0.20$
(2) Weedy *vs.* Bare: $P > 0.20$
(3) Shrubby *vs.* Bare: $P > 0.60$

The total number of small mammals for the three types of fence rows are: weedy—65, shrubby—56, bare—44. Four species of small mammals were caught: *Peromyscus maniculatus* (Wagner), *Microtus montanus* Peale, *M. longicaudus* (Merriam) and *Sorex vagrans* Baird. The totals of these four species in the three types of fence rows are shown in Table II.

Discussion

There was no statistically significant difference among total small mammal populations of the three types of fence lines studied.

Microtus montanus was more abundant in the weedy type than in either the brushy or bare types.

Peromyscus maniculatus was equally abundant in all three types.

Sorex vagrans samples and *Microtus longicaudus* samples were not large enough for characterization.

It can be concluded from the above that *Microtus montanus* is favored by the greater density of cover near the

TABLE II. Summary of data by species

	Weedy	Shrubby	Bare
Peromyscus maniculatus	45	46	42
Microtus montanus	17	5	2
Microtus longicaudus	0	4	0
Sorex vagrans	3	1	0

TABLE III. Summary of weather records

Date	Weather	No. of catches
X/20	cold, clear	28
X/23	warm, fairly humid	24
X/27	warm, very humid	46
X/30	very warm, mostly clear	67

ground which is found in the weedy type. This is a result of the greater diurnal activity of *M. montanus*, and thus its requirement for denser cover (Rickard, 1957). The same source states that *Peromyscus* prefers open stands of little resistance to movement across the ground; this might explain its dominance in these fields, all cleared of cover.

Microtus montanus was found to be more abundant than *M. longicaudus*. This is in agreement with Rickard (1957) who found that in virgin stands *M. longicaudus* was more abundant, but in disturbed (weedy) stands *M. montanus* was more abundant.

Weather data for the nights of the trapping (courtesy of Dr. Glenn Horner, S.C.S., Pullman) are given in Table III.

Results correlate well with the effects reported by Youngman (1956) and by Gentry & Odum (1957). The former reported that mice were more active, and moved farther, on dark nights than on clear nights; while the latter noted that warm, cloudy conditions increased, cold and clear decreased, their catches. Here is a variable which might well be taken into account in designing studies of the present sort.

SUMMARY

Trapping of small mammals along shrubby, weedy, and bare fence lines in Whitman County, Washington, all bordered by tilled fields, showed that the small mammal populations were nearly equal in the first two but lower in the last. *Peromyscus maniculatus* was present in almost equal numbers in each fence type. *Microtus montanus* was most abundant in the weedy fence rows, sparsely present in the shrubby fence rows, and rare in the bare fence rows. This is interpreted as a cover effect.

REFERENCES

Booth, Ernest S. 1949. How to know the mammals. 206 pp. Wm. C. Brown, Dubuque, Iowa.

Daubenmire, R. F. 1942. An ecological study of the vegetation of southeastern Washington and adjacent Idaho. Ecological Monog. **12**: 53-79.

Davis, William B. 1939. The recent mammals of Idaho. 400 pp., Caxton Printers, Caldwell, Idaho.

Gentry, J. B., and E. P. Odum. 1957. The effect of weather on the winter activity of old-field rodents. Jour. Mammal. **38**: 72-77.

Rickard, W. H. 1957. Distribution of small mammals in relation to vegetation patterns. Ph.D. Thesis, State College of Washington.

Snedecor, George W. 1956. Statistical methods. 5 ed. 534 pp. Iowa State College Press, Ames, Iowa.

Youngman, P. M. 1956. Ecology of the striped field mouse, *Apodemus agrarius coreae*, in central Korea. J. Mammal. **37**: 1-10.

R. T. OGILVIE
THOMAS FURMAN

DEPARTMENT OF BOTANY
STATE COLLEGE OF WASHINGTON
PULLMAN, WASHINGTON

THE COMPETITIVE EFFECT OF DANTHONIA SPP. ON THE ESTABLISHMENT OF *BOTHRIOCHLOA AMBIGUA*

INTRODUCTION

Bothriochloa ambigua S. T. Blake, a native perennial grass of limited grazing value, has invaded Danthonia dominant pastures over wide areas of the southern tablelands and southwest slopes of New South Wales (Moore 1953, 1957). Roe (1947) has reported Bothriochloa as a frequent dominant in the pastures of the New England region, where it readily colonizes cultivated areas that are allowed to revert to pasture, and commonly invades the natural sward. Field observations suggest that Bothriochloa invades the native pastures where the Danthonia sward has been weakened by overgrazing, while in a pasture where the perennial grasses remain vigorous, it is either absent or present as a minor species only.

Moore (1957) showed that significant changes in certain soil properties follow invasion by Bothriochloa, but there was no evidence to suggest that soil texture *per se* was a limiting factor in establishment. A study of germination and seedling root growth (Moore 1958) indicated that, if both Bothriochloa and *Danthonia* spp. were available to colonize a bare area, the former species would probably have an initial advantage because of its more vigorous root growth.

The primary objective of the present study[1] was to determine the effect of *Danthonia* spp. on the establishment of Bothriochloa. Under pasture conditions the *Danthonia* spp. are likely to be weakened by sheep grazing, and it appears that during abnormally wet years Bothriochloa spreads more rapidly than during periods of normal rainfall. Two treatments were therefore superimposed after initial establishment of the two grasses. The Danthonia was clipped at intervals, to simulate grazing, and two levels of moisture were included.

MATERIALS AND METHODS

To avoid water-logging, a permeable sandy loam was selected for the growth medium, and placed in boxes 12 in.

[1] The author is indebted to Mr. G. A. McIntyre, Biometrics Division, C.S.I.R.O., for assistance with the statistical treatment of the results; and to Mr. W. A. Bruce, Division of Plant Industry, C.S.I.R.O., for technical assistance.

× 12 in. × 8 in. deep. To determine the effect of Danthonia on the establishment of Bothriochloa, four conditions were imposed, viz.

(1) Bothriochloa seed (22 per box) sown in bare soil.
(2) Danthonia seed (61 per box) and Bothriochloa seed (22 per box) sown simultaneously in bare soil.
(3) Danthonia plants established at high density (61 per box) and Bothriochloa seed (22 per box) sown amongst them.
(4) Danthonia plants established at low density (13 per box) and Bothriochloa seed (20 per box) sown amongst them.

The arrangement and spacing of the plants is shown in Figure 1. For conditions 3 and 4 Danthonia clones were collected in the field, broken into uniform segments, and planted at the two densities on October 16, 1956.

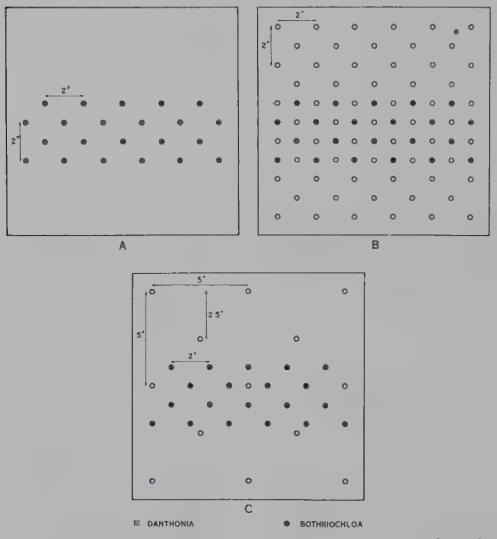


FIG. 1. Arrangement of plants in boxes A. *Bothriochloa* seed on bare soil. B. *Bothriochloa* seed with either *Danthonia* seed or *Danthonia* plants at high density. C. *Bothriochloa* seed with *Danthonia* plants at low density.

To achieve reasonable uniformity in establishment of the seedlings, the seed of both grasses was set out to germinate in Petri dishes on December 4, 1956. Transference of germinated seed to the soil was commenced on December 6, 1956, and continued for the subsequent 12 days when it was clear that no viable seed remained. It had originally been intended to sow the Bothriochloa seed over the whole soil surface in the boxes, but the amount of viable seed available was sufficient for only 4 rows per box.

For each of the above conditions there was superimposed a high and low moisture treatment, and, except for condition (1), clipping of the Danthonia was compared with no clipping. These 14 treatments were replicated 6 times in a randomized block design.

The differential watering was commenced on February 4, 1957. In the high moisture treatment the soil was kept moist by daily watering, while water was added to the low moisture treatment when the moisture content of the soils was at or near wilting point. The Danthonia was clipped to about ¼ in. above the soil surface on November 1, 1956, February 4, 1957, and November 21, 1957.

Several species of Danthonia were used, both as plants and as seed. These were *D. auriculata* J. M. Black, *D. carphoides* F. Mueller ex Benth and *D. pilosa* R. Br. No attempt was made to use a single species, as it was intended that the mixture should approximate that occurring in the field. At the time of collection of the plants, identification of the species would in any case have been difficult if not impossible because flowering had not commenced.

On March 12, 1957, tiller counts of the Bothriochloa plants were made, and the mean number of tillers per plant determined. On March 26, 1957, and again on February 14, 1958, an estimate of ground cover of Bothriochloa was made, using a point quadrat with ten points spaced at one inch intervals. By rotating the quadrat through 360°, the number of hits for ten positions was recorded, making a total of 100 points per box. The total number of hits recorded per box therefore gave an estimate of the percentage cover of the Bothriochloa.

RESULTS

An analysis of the data shows no significant difference between high and low water, or between clipping and non-clipping of the Danthonia; nor was there any interaction between Danthonia density, water treatment or clipping treatment. The mean figures for the clipping and water treatments at each of the Danthonia densities can therefore be pooled, when it is seen that highly significant effects of Danthonia density were obtained.

On March 12, 1957, there was no difference in the number of tillers per plant between those Bothriochloa seedlings established on bare soil and those established simultaneously with Danthonia seedlings. Tiller number was significantly reduced by established plants at both high and low densities (Table I).

TABLE I. Mean number of tillers per plant of *B. ambigua*

Danthonia Density	High Water		Low Water		General Mean*	No. of Replications
	Danthonia Clipped	Danthonia not Clipped	Danthonia Clipped	Danthonia not Clipped		
Nil	5.87		7.22		6.55	12
Seed	5.98	6.23	6.58	5.85	6.16	24
Plants-High Density	1.60	1.47	1.93	1.65	1.66	24
Plants-Low Density	4.70	3.72	4.30	3.88	4.15	24

*L.S.D. between means of 24: 5%, 0.717; 1%, 0.95; 0.1%, 1.24
*L.S.D. between means of 12 and 24: 5%, 0.88; 1%, 1.16; 0.1%, 1.52

Ground cover of Bothriochloa is greatly reduced by Danthonia plants at high density. (Table II and III.) There is a significant reduction in the ground cover of Bothriochloa due to Danthonia seedlings and to Danthonia plants at low density, but the effect is much less marked than that of Danthonia plants at high density.

DISCUSSION

The results fully support previous suggestions (Moore 1953, 1957) that invasion of native pastures by Bothriochloa follows over-grazing and weakening of the Danthonia sward. The marked competitive effect of established Danthonia plants at high density on the Bothriochloa seedlings would be anticipated, as would also the lesser effect of Danthonia plants at low density.

TABLE II. Mean percent ground cover of *B. ambigua* by point quadrat analysis (26/3/57)

Danthonia Density	High Water		Low Water		General Mean*	No. of Replications
	Danthonia Clipped	Danthonia not Clipped	Danthonia Clipped	Danthonia not Clipped		
Nil	30.2		27.3		28.8	12
Seed	26.8	15.5	18.7	24.2	21.3	24
Plants-High Density	4.5	4.3	6.7	4.0	4.9	24
Plants-Low Density	21.3	20.3	19.3	18.0	19.7	24

*L.S.D. between means of 24: 5%, 4.96; 1%, 6.58; 0.1%, 8.57
*L.S.D. between means of 12 and 24: 5%, 6.08; 1%, 8.06; 0.1%, 10.49

TABLE III. Mean percent ground cover of *B. ambigua* by point quadrat analysis (14/2/58)

Danthonia Density	High Water		Low Water		General Mean*	No. of Replications
	Danthonia Clipped	Danthonia not Clipped	Danthonia Clipped	Danthonia not Clipped		
Nil	35.33		26.17		30.75	12
Seed	26.33	19.00	20.83	19.67	21.46	24
Plants-High Density	8.17	6.50	11.00	10.17	8.96	24
Plants-Low Density	22.83	22.33	20.67	21.67	21.87	24

*L.S.D. between means of 24: 5%, 4.66; 1%, 6.18; 0.1%, 8.04
*L.S.D. between means of 12 and 24: 5%, 5.71; 1%, 7.56; 0.1%, 9.85

However, when seed of both species is available to colonize a bare area, it is clear that Danthonia seedlings can exert only a limited effect on the Bothriochloa, insufficient to prevent the latter from becoming the dominant species in the sward. This is in agreement with the suggestion put forward by Moore (1958) that the more vigorous root growth of Bothriochloa seedlings as compared with those of Danthonia gives the former an initial advantage when growing in competition with the latter.

It would appear that the mechanism of action of Danthonia in competition with Bothriochloa lies within the root zone. At no time was the top growth of the Danthonia sufficient to cause effective competition for light. Since the moisture content of the soil had no effect on the growth of Bothriochloa after it had become established, competition between the two grasses for water can be eliminated. Other possible causes are competition for one or more nutrients, or the production of a root exudate by Danthonia which inhibits growth of Bothriochloa.

Although clipping of the Danthonia had no significant effect on the development of Bothriochloa, it can be seen from Tables I-III that there was a tendency for the growth of Bothriochloa to be greater under the clipping treatment than under the non-clipping treatment. Clipping would cause a decrease in the amount of root material, and hence reduce the competitive effect of the Danthonia. Under normal grazing conditions it is probable that this effect would be more significant because of the more frequent removal of the Danthonia tops. The growth of the Danthonia in the boxes was too slow to allow frequent clipping. It is probable that the technique used in this work did not produce a sufficient difference in moisture supply to the plants, as water was added whenever critically low levels were reached. This was necessary to prevent the entire loss of the low water treatment. This would explain the fact that no effect of water supply on the development of Bothriochloa was observed. Under field conditions, the effect of moisture supply might be significant. However as both Bothriochloa and Danthonia are capable of withstanding long periods of drought, it is likely that any effect of moisture would be operative chiefly during the initial stages of establishment rather than after successful establishment has been achieved.

SUMMARY

Bothriochloa ambigua was grown in competition with Danthonia seedlings, and with Danthonia plants which were established at two densities. Two water levels were used, and two clipping treatments applied to the Danthonia. The development of the Bothriochloa was measured by tiller counts and by estimation of ground cover, using the point quadrat.

The number of tillers per plants was not affected by Danthonia seedlings, but was reduced by established Danthonia plants at both high and low densities, the reduction being much greater at the high density.

Ground cover of the Bothriochloa was significantly reduced by Danthonia plants at both high and low density, as well as by Danthonia seedlings. The effect was again much greater at the high density of Danthonia plants. There was no significant difference between Danthonia seedlings and Danthonia plants at low density in their effect on the ground cover of the Bothriochloa.

No significant effects due to water level or to clipping of the Danthonia were obtained.

The results indicate that invasion of a native pasture is not likely to occur unless the *Danthonia* spp. are weakened by overgrazing.

When seed of Danthonia and Bothriochloa are both available at the same time to colonize a bare area, the competitive effect of the former is not sufficient to prevent the development of Bothriochloa dominance.

REFERENCES

Moore, C. W. E. 1953. The Vegetation of the South-eastern Riverina, New South Wales. II. The disclimax communities. Aust. J. Bot. **1**: 548-567.

——. 1957. A study of some soil properties in relation to the invasion of native pastures by *Bothriochloa ambigua* S. T. Blake. Aust. J. Bot. **5**: 44-51.

——. 1958. Germination and seedling root growth of *Bothriochloa ambigua* in relation to invasion of native pastures. Ecology **39**: 367-371.

Roe, R. 1947. Preliminary survey of the natural pastures of the New England district of New South Wales and a general discussion of their problems. Counc. Sci. Industr. Res. Aust. Bull. No. **210**.

C. W. E. MOORE
COMMONWEALTH SCIENTIFIC AND INDUSTRIAL RESEARCH ORGANIZATION,
DIVISION OF PLANT INDUSTRY,
CANBERRA. A.C.T.

UPPER LIMITS OF VEGETATION ON MAUNA LOA, HAWAII[1]

There seems to be almost no carefully recorded information on the vegetation on the upper slopes of the Mauna Loa volcano, on the island of Hawaii. Skottsberg (1931) discussed the flora of the high Hawaiian volcanoes, Bartram (1933) mentioned the occurrence of a moss on the summit of the mountain, and Hartt and Neal (1940) gave an account of the neighboring, but rather different, Mauna Kea. Robyns and Lamb (1939, pp. 267-268) gave the most adequate description of this area. The following notes are by no means a complete account, but, in the absence of a careful systematic study, may be of interest.

Through the courtesy of Dr. Chester K. Wentworth I was able on January 5, 1958, to drive up to the High Altitude Laboratory of the U. S. Weather Bureau, situated at 11,134 ft. on the north slope of Mauna Loa, facing Mauna Kea. On the way down, notes on the vegetation were taken in conjunction with altimeter readings.

The north slope of Mauna Loa is a bleak waste of interlaced lava flows of various ages. The road to the Weather Bureau Station is relatively new, graded and bulldozed into the rough lava. It spirals on a rather gentle grade up the mountain from Kulani around to the west, overlooking the Humuula Saddle between Mauna Loa and Mauna Kea. The lower part of the road runs through fine wet forest of *Metrosideros,* much of which, unfortunately, is being destroyed and the land converted for grazing purposes. This forest decreases somewhat in stature upward on the mountain slope, but irregularly, depending on the age and character of the lava substratum. It ends abruptly where the 1942 lava flow cuts across the road at about 6500 ft.

After this there is intermittent woodland of low stature with scrub in the openings. This is the mountain parkland formation of Robyns and Lamb. The scrub component is the typical montane xerophytic vegetation of the medium high slopes of the larger volcanoes of the islands—Mauna Loa, Mauna Kea, Hualalai, and Haleakala, starting in the upper edges of the forest at different altitudes, depending on the exposure. This scrub reaches to the summit of Haleakala, Maui, and to different altitudes on the volcanoes on the island of Hawaii, apparently depending at least in part on substratum. It may be prevented by continuous low temperature from reaching the highest altitudes on Mauna Kea where the conditions otherwise might be favorable (see Hartt and Neal (1940, pp. 242-243)). It is characteristically composed of *Styphelia, Vaccinium, Dubautia, Geranium, Coprosma, Dodonaea,* small *Metrosideros,* and occasionally other genera. This is the subalpine belt of the zonation recognized by Skottsberg and by Hartt and Neal, the subalpine shrub zone of Robyns and Lamb, and the E_2 zone of Ripperton and Hosaka. In structure this scrub is microphyllous, 1-2 m. tall, and from open to nearly or quite closed, but usually rather sparse.

As the road climbs stretches of lava become more prevalent, usually of the rough, clinkery "aa" type, less often of the smooth or ropy "pahoehoe" type. The vegetation becomes more and more reduced to small "islands" or "kipukas" of older surfaces surrounded by newer lava with little vegetation. These kipukas may be very small or up to many acres in extent. The vegetation is commonly open woodland of scrubby *Metrosideros* up to 3-5 m. tall, with scrub such as described above between the trees, which are sometimes scarce or lacking. The highest trees and well developed scrub along the road are in kipukas at 8250 to 8300 ft. The scrub here has a number of species in the above mentioned genera.

Above this level are extensive aa lava fields with scattered kipukas of older pahoehoe lava. Shrubs are fairly numerous in these kipukas, but do not form a continuous vegetation, and are only occasional on the aa around the kipukas, becoming very rare or absent on aa above 8300 ft. They are mainly *Vaccinium* with some *Styphelia douglasii* and *Dubautia.* Above 8300 ft. the aa lava is practically without visible plant life except for occasional tufts of a gray moss in pockets.

Crossing the aa fields at about 8500 ft. and 8700 ft. are two fresh-looking flows of black shiny pahoehoe lava of low rounded relief. These have a few scattered *Vaccinium* bushes with occasional *Styphelia* and *Dubautia.* At 8800 ft. are two small kipukas of an older pahoehoe with fairly abundant shrubs of the same three genera and tufts of a grass, *Trisetum glomeratum. Dubautia ciliolata* var. *juniperoides* (Gray) Keck reaches its highest observed station here (no. 39296).[2] This vegetation is mainly on the pahoehoe but has slightly invaded the aa around the edges.

Above this are broad fields of fresh looking aa. The last lichens were noticed at 9100 ft., but they had not been common even well below this elevation. Between 9100 and 9200 ft. *Vaccinium* is rather frequent on light brownish weathered pahoehoe and *Styphelia douglasii* (no. 39297) is occasional and reaches its upper limit here. Between 9200 and 9300 ft. these shrubs are at best widely scattered, but on pahoehoe a number of individuals are likely to be seen in any field of vision. Above 9300 ft. shrubs are very local or absent. At 1400 ft. a population of 6 individual *Vaccinium* shrubs is seen, both *Vaccinium reticulatum* Sm. (nos. 39301, 39303) and *V. peleanum* Skottsb. (nos. 39299, 39300, 39302). *Rhacomitrium,* the gray moss is common here in north-facing cracks.

At about 10,000 ft., on a tiny patch of rather rough pahoehoe, surrounded by aa, were two small gnarled *Vaccinium reticulatum?* (no. 39304) bushes, the highest woody plants seen along the road. *Pellaea ternifolia* is fairly common here in crevices. This is also the highest spot where *Rhacomitrium,* or any plant, was seen on aa lava.

From 10,000 up to 11,150 ft is mostly aa lava with occasional exposures of an older pahoehoe. The surface of the pahoehoe is somewhat checked and cracked, the cracks showing up because of an efflorescence of white mineral. On an exposure of this type at 10,550 ft. the gray moss is very common in north-facing crevices, and a specimen from here was determined by H. A. Miller as *Rhacomitrium lanuginosum* var. *pruinosum* Hook. & Wils. (no. 39307). The fern, *Pellaea ternifolia* (no. 39305), and the grass, *Trisetum glomeratum* (no. 39306), are occasional here in very small tufts in crevices at any angle of exposure, but mostly exposed upward. These crevices are either quite deep or are covered by an accumulation of small rock debris which protects the root crowns and rhizomes from undue desiccation.

On a similar elongate pahoehoe exposure crossing the road at 10,800 ft. *Rhacomitrium* is again common in north-facing crevices. It was noticed that none of the tufts were exposed to the direct sun at 4:00 p.m. but that

[1] Publication authorized by the Director, U. S. Geological Survey.

[2] Numbers refer to Fosberg collections, deposited in the U. S. National Herbarium.

some were beginning to be hit by the sun at 4:15. Near the top of this exposure at perhaps 10,950 or 11,000 ft. tufts of *Trisetum* were seen, but no *Pellaea*. Another such exposure of pahoehoe continued on up the slope beyond a short stretch of aa, but time was not available to examine it. In all probability at least the moss would have been present there, as it showed no signs of becoming scarcer or less vigorous up to the top of the lower exposure. However, on pahoehoe of similar character at perhaps 11,160 to 11,200 ft. just above and beyond the weather observatory no plants at all, not even moss, were seen.

Time was not available for exploration farther up the mountain. However, Miller informs me that he has collected *Rhacomitrium* at 11,500 ft. on this same road and Bartram (1933, p. 101) recorded it from the summit of Mauna Loa at 13,600 ft., collected by Brumaghim, so it is probably found in suitable sheltered crevices on pahoehoe lava all the way up.

One interesting observation about these high-altitude occurrences of plants is that there seems to be no ecological relation or dependence between them, whatever. The moss, fern, grass and shrubs occur in separate niches or in isolated examples of the same niche. The moss does not seem in any way to precede or prepare the way for the higher plants, nor the fern and grass to prepare the habitat for the shrubs. Cracking of the lava seems to be the only requisite or preparation required for any of them, and this is the result either of the original cooling or of frost. This lack of interdependence is probably the outstanding characteristic of the true alpine zone on Mauna Loa. Even the influence of man is not in any way apparent. The highest introduced plant seen, *Hypochoeris radicata* L., was at 8100 ft. (no. 39,298). The only evident control of the vegetation above about 8300 ft. is by the physical environmental complex.

Comparison with data available on the vegetation of Mauna Kea shows that the upper limits of individual plant species as well as of the corresponding vegetation types or zones are generally higher on Mauna Kea than on Mauna Loa. For example, Robyns and Lamb quote Hillebrand as giving the upper limit of the upper forest zone on Mauna Kea as 11,000 ft. and Hartt and Neal give timberline there as 9500 ft., but the highest trees seen by me on Mauna Loa were 8300 ft. The highest shrub on Mauna Kea was seen by Hartt and Neal at 12,250 ft., while the highest seen by me on Mauna Loa was 10,000 ft. The highest vascular plant seen on Mauna Kea by Hartt and Neal, *Trisetum glomeratum*, was at 13,400 ft., and on Mauna Loa I saw the same species, also the highest vascular plant, at 11,000 ft.

Upper limits of alpine zone species are shown in Table I.

TABLE I. Upper altitudinal limits, in feet, on Mauna Loa and Mauna Kea.

	Mauna Loa Fosberg	Mauna Kea
Asplenium adiantum-nigrum L.	not seen	13,500 (Judd; fide Hartt & Neal)
Pellaea ternifolia (Cav.) Link	10,550	10,400 (Hartt & Neal)
Trisetum glomeratum (Kunth) Trin.	11,000	13,400 " "
Agrostis sandwicensis Hbd.	not seen	13,100 " "
Vaccinium peleanum Skottsb.	9,400	12,250 " "
Vaccinium reticulatum Sm.	10,000	not seen
Styphelia douglasii (Gray) F. Muell.	9,150	11,600 " " (as *Styphelia* sp.)
Coprosma montana Hbd.	not seen	10,400 (Skottsberg)
Argyroxiphium sandwicense DC.	not seen	12,250 (Hartt & Neal)
Dubautia arborea (Gray) Keck	not seen	9,750 (Skottsberg)
Dubautia ciliolata (DC.) Keck	8,800	9,900 "
Dubautia strutholoides (Gray) Keck	not seen	11,375 "
Tetramolopium humile (Gray) Hbd.	not seen	Alpine zone, acc. Hartt and Neal but no altitude given.

Introduced species found in the Alpine zone of Mauna Kea by Hartt and Neal were *Anthoxanthum odoratum* L., *Poa annua* L., *Poa pratensis* L., *Rumex acetosella* L., *Cirsium vulgare* (Savi) Airy-Shaw, *Sonchus oleraceus* L. (found by Rock at 12,000 ft.), *Senecio sylvaticus* L., and *Taraxacum officinale* Weber. On Mauna Loa no introduced plants were found in the Alpine zone; the highest being that mentioned above, *Hypochoeris radicata*, near the upper edge of the Subalpine at 8100 ft.

An explanation for the generally better development of vegetation at higher altitudes on Mauna Kea compared with Mauna Loa is probably to be sought in two factors—the prevalence of ash rather than fresh lava on Mauna Kea, and the much greater age of the substratum on Mauna Kea, with consequently greater weathering and more advanced soil formation. On the portions of Mauna Loa observed the lava was all relatively recent.

A few comments on the bearing of these observations on the vegetation classifications adopted by previous writers may be of interest. Skottsberg's paper (1931) is mainly a floristic account and mentions the vegetational aspects only incidentally. He regards timber line as an important boundary but does not describe its occurrence. Hartt and Neal also speak of timber line, and talk about it at length but do not describe it in a way that gives any clear idea of where it is or how definite it is. On Mauna Loa nothing like a true timber line was observed, though one may exist on some parts of the mountain. The mosaic of recent interlacing lava flows of varied ages would not give much reason to expect a timber line in the sense that it exists on mountains of other sorts.

There seems to be general agreement that an Alpine and a Subalpine zone should be recognized. Skottsberg, Hartt and Neal, and Robyns and Lamb all regard the Alpine zone as that above timber line and the Subalpine zone as the Upper Forest Zone of previous authors.

Robyns and Lamb, in addition, give altitudinal limits of 7,000 to 9,000-10,000 ft. for the Subalpine zone and above this for the Alpine zone. They also interpose a Parkland zone between the Mountain forest zone and the Subalpine zone which obviously is the lower part of the Subalpine of Skottsberg and Hartt and Neal. Ripperton and Hosaka (1942) treat the high mountain area only incidentally, as it is not suitable for pasture. They do not name their zones but their Zone E corresponds to the Subalpine and Alpine, combined, and they divide this into three numbered subdivisions, E_3 being the Alpine zone of the other authors, the two others being differentiated as being "open forest and shrub" (E_1) and "mainly upland open shrub" (E_2). They are distinguished altitudinally, also, but the stated altitudinal limits of E_1 4,000-7,000 ft.; E_2 7,000-10,000 ft.; and E_3 over 10,000 ft. seem not to hold up at all well on their map. There seems little doubt, however, that their zones which actually correspond rather well with those of Robyns and Lamb, do represent real differences in aspect of the vegetation.

As might be expected at such a level of generalization some contradiction and inconsistency exist both within and between these systems of zones, as when Robyns and Lamb (1939, p. 275) give the upper limit of tree growth as about 7,000 ft. and on p. 244 quote Hillebrand as saying that the upper forest zone extends up to 6,000 or 9,000 or, on Mauna Kea, to 11,000 ft. Hartt and Neal give 9,500 ft. as the altitude of timber line on the same mountain.

Along the road above Kulani on Mauna Loa the Parkland zone would extend from somewhat above 6,500 ft. to perhaps 8,300 ft., though the greater part of this area is bare lava. The Subalpine Shrub zone would be from 8,300 ft. to perhaps 10,000 ft., with scattered shrubs only and the greater part of the area again bare lava. This manifestation of the montane scrub vegetation of these volcanoes is sparse, indeed, and it may be questioned whether much clarity is gained by placing this scattering of shrubs in the same zone with the much denser scrub vegetation of, for instance, Haleakala volcano, Maui. However, there do seem to be definite altitudinal limits to shrub growth on Mauna Loa and they are much lower than on Mauna Kea.

The areas above the limits of shrub growth are described by Robyns and Lamb, and following them, by Ripperton and Hosaka, as belonging to the "Moss-Lichen formation," though it is not too clear that this formation does not include also part of the area characterized by shrubs. They start by saying "Above all the zones of seed bearing plants" but continue by mentioning several seed plants, as well as ferns and mosses, and then mention a moss as extending to the summit of Mauna Loa. Then they say "Above the Moss-Lichen formation on Mauna Loa are extensive fields of barren lava extending to the top of the mountain." This does not add up to a very satisfactory picture of what they regard as comprising this formation. It is notable that in spite of their terms "Moss-Lichen Formation" and "Alpine Moss-Lichen" no lichens are mentioned, nor were any observed in this area on Mauna Loa. In their terminology they are apparently following the terminology of Clements in his "general classification of climax formations." This may possibly be justified in the interests of generalization and of regional correlation. However, it is only proper to point out that the terminology is, in this case, somewhat misleading. It is also well to point out that this entire situation is an excellent example of the subjective nature of this kind of generalization resulting in formulation of major categories of vegetation and of life zones or vegetation zones. These are excellent tools to further understanding of natural situations, but it should never be assumed that such terminology can be carried over from one worker to another without redefinition or clear reference to examples.

F. R. Fosberg

U. S. Geological Survey
Washington, D. C.

References

Bartram, E. B. 1933. Manual of Hawaiian mosses. Bishop Mus. Bull. **101**: 1-275.

Hartt, C. G. and M. C. Neal. 1940. The plant ecology of Mauna Kea, Hawaii. Ecology **21**: 237-266.

Ripperton, J. C. and E. Y. Hosaka. 1942. Vegetation zones of Hawaii. Hawaii Agr. Expr. Sta. Bull. **89**: 1-60.

Robyns, W. and S. H. Lamb. 1939. Preliminary ecological survey of the island of Hawaii. Bull. Jard. Bot. Bruxelles **9**: 241-293.

Skottsberg, C. 1931. Remarks on the flora of the high Hawaiian volcanoes. Acta Horti Gothob. **6**: 47-65.

SOME PALEOBOTANICAL ASPECTS OF TUNDRA DEVELOPMENT

Tundras or tundra-like landscapes are probably as old as land vegetation itself. Any evidence of past glaciation is indicative of conditions under which tundras could have developed. There is no reason to doubt that there were tundras in the Precambrian, and they must have been expansive during the Permian. Even during those relatively warm intervals, such as the Pennsylvanian and the late Eocene, small tundralike environments must have existed at high altitudes. However, if we try to speculate on the kinds of plants that covered a Precambrian or Pennsylvanian tundra, even reasonable guesswork is impossible.

In narrating the chain of events that led to the expansion of those tundras that today cover 26% of the surface of the land, we must go back to the early part of the Tertiary period. During the late Eocene and early Oligocene, worldwide warmth which began to manifest itself in the late Cretaceous reached its maximum. Tropical and temperate plants were able to thrive far north of their present ranges. For example, imprints of huge palm leaves, along with an abundance of foliage of other plants that thrive today only in warm places, are prominently displayed in the Eocene rocks of northwestern Washington and adjacent Canada. A boreal unit of the temperate Tertiary flora was discovered many years ago in Grinnell Land only 8.5 degrees from the North Pole (Heer 1878). It contained fragmentary leaves of Metasequoia or Taxodium, Pinus, Picea, Cercidiphyllum, and betulaceous leaves resembling Corylus. This florule probably thrived during the late Eocene. Farther south, but still above the Arctic Circle, are several other floras of temperate and cool-temperate aspect that have been described in detail by Heer, Nathorst, Seward, and Kryshtofovich.

The circumpolar distribution of temperate and boreal Tertiary floras has been used as an argument against

theories of shifting poles and massive movements of continents to provide suitable climates for these floras in the far north. Chaney (1940) has pointed out that if the North Pole was located in the north Pacific Ocean during any part of the Eocene epoch, where some European climatologists would have placed it, North American Tertiary floras would have frozen. A whole sequence of fossil floras, ranging in age from Upper Cretaceous to Pliocene, occurs between Vancouver Island and northern California, and at no place in this sequence of floras is there any indication of the frigid climates that would have been foisted upon that region had the pole at any time been situated just over the western horizon.

Following the Eocene, that epoch during which subtropical floras extended into southern Alaska, the middle Oligocene marks the beginning of a reversal of the climatic trend of the early stages of the Tertiary. Fossil plants of the later Oligocene deposits show development of cooler climates in the far north. With the passing of time this coolness increased, and it continued to increase into and through the latter half of the Tertiary period, and finally culminated in the Pleistocene ice age. By Miocene time temperate floras had disappeared from the arctic and subarctic latitudes, and tropical floras had become compressed into a narrower belt mostly within low latitudes. This retreat continued into the Pliocene and by the end of that epoch north temperate zone floras had become established along essentially the same plan as they are today. Thus we can designate the Pliocene as the time interval during which the last stages of the transformation from middle Tertiary to modern temperate and boreal vegetation took place. Our modern temperate flora is essentially a late Pliocene flora modified to some extent by conditions of the Pleistocene ice age.

The phenomena and events I have briefly outlined have some bearing on the development of modern tundras. During the time of maximum warmth (the late Eocene and early Oligocene) complete absence of polar ice caps is probable, and expanded tundras of the type that now cover much of the North American and Eurasian land masses did not exist. But tucked away at high altitudes there were, in all probability, numerous small isolated tundralike areas along the edges of and at the ends of mountain glaciers. These were presumably only narrow strips of land conceivably only a few feet wide at places that were perennially chilled by the ice, but they were wide enough to maintain localized tundra floras. With the increasing coolness of the middle and late Tertiary, these small tundra strips with their specialized floras stretched down from the high valleys and finally merged with each other on the lowlands. They expanded rapidly once the broad level arctic plains were reached, and ultimately they developed into circumpolar tundra belts. As the tundras spread over the vast expanses of land abandoned by the retreating boreal vegetation, some remnants of the latter managed to survive for varying periods of time in protected places. Some of these stranded species adjusted themselves to the inhospitable environment and became incorporated into the tundra flora. Probably most present tundra and subtundra genera or families whose principal centers of distribution are now in boreal and temperate regions belong to this category. Thus from small beginnings in the mid-Tertiary, tundras continued to expand throughout the late Tertiary, and by the end of Pliocene time modern tundra floras, as part of the vegetational pattern of the Northern Hemisphere, had become established essentially as they are today.

Unfortunately we possess very little direct information on arctic vegetation of the latter half of the Tertiary period, and extremely few fossil representatives of the more typical tundra plants have been found in deposits older than Pleistocene. Those floras that were described many years ago from Greenland and other far northern regions, and believed by Heer and some of his successors in paleobotanical research to be of Miocene age, are now known to be Eocene or Cretaceous. They apparently represent arctic vegetation of the times of maximum warmth. However, Lindquist (1947) has reported two Miocene birches from Iceland. One appears to represent a hybrid of *Betula callosa* and *B. tortuosa*, and the other a cross between either of these species and *B. nana*. He concludes that the subarctic *B. callosa* has undergone little change since the Miocene.

To my knowledge no plants are known from the Pliocene of arctic regions, and the discovery of such would be an event of significance. However, an arctic Pliocene flora could readily pass unrecognized in absence of supporting evidence as to age. Pliocene floras in general are not as well known as those of the other epochs of the Tertiary because of climatic, topographic, lithologic, and other factors that effect the fossil record.

Although we have but little direct evidence that bears on arctic Pliocene vegetational history, it is certain that the development of tundra vegetation during this epoch was the result of lowered temperatures which were responsible for the replacement of boreal species with more dwarfed and hardy types. Such a change is actually recorded in later formed deposits farther south. In the Cromer forest in Norfolk, which is generally regarded as of uppermost Pliocene age, there is a flora of 135 species which seems to differ little from that of the same part of England today. Above it, in a layer of clay believed to represent the basal Pleistocene, is the "Arctic Plant Bed," which contains *Salix polaris*, *Betula nana*, and a characteristic species of arctic moss. This succession is especially significant in that it apparently recapitulates the change that had taken place a little farther north at an earlier time. In other words, it is a specific and concrete example of the replacement of a cool temperate by a tundra flora.

Our understanding of arctic, subarctic, and boreal Pleistocene vegetation is much more extensive than that of the Pliocene. The interglacial floras of the British Isles are especially well known. One of those from the Cam Valley near Cambridge contains 89 species and includes such characteristic tundra components as *Betula nana, Carex capitata, Eriophorum latifolium, Dryas octopetala*, and *Salix polaris*. Its only elements in common with the Cromer flora are 15 widely ranging species, several of which are aquatics. One of the classic Pleistocene arctic floras was described by Heer (1871) many years ago from Spitzbergen. It contains *Salix polaris, S. retusa, Betula nana*, and *Dryas integrifolia*. One of the very few North American Pleistocene arctic floras has been described by Chaney and Mason (1936) from Fairbanks, Alaska. The 27 species recognized there include *Picea glauca*, Carex, Eriophorum, four species of Salix, *Populus tremuloides*, two betulas and several herbs. A species of Silene is the only plant that does not grow near Fairbanks today. The circumpolar *Empetrum nigrum* has been found in the Neolithic, late glacial, and interglacial deposits of Great Britain (Reid, 1899; Matthews, 1955) but nothing is known of its earlier history.

In summary and conclusion it may be said that the present flora of the arctic tundra of the Northern Hemisphere probably developed during the Pliocene, and at the end of that epoch existed essentially in its present

form. We can assume, however, that it suffered some disturbance during the Pleistocene ice age. The essential components, such as *Empetrum nigrum* and *Dryas octopetala*, are probably, at the latest, pre-glacial in origin. The dwarf willows and birches probably came in during the late Cretaceous or early Tertiary, as did presumably the northern pines and spruces of the subtundra. There are other plants which the fossil record shows to have abandoned northern latitudes for more congenial surroundings when the tundra took over. For example, *Metasequoia* and *Taxodium* probably originated in the far north during favorable climatic intervals of the mid-Mesozoic. Also the abundance of fossil ginkgos and related plants in Mesozoic arctic rocks points to a northerly origin for this group. Migration saved some of these from complete extinction. Knowledge of the pre-Pleistocene history of the most typical tundra species is severely limited because of the scant fossil record of late Tertiary vegetation in the Arctic. The newly developed science of palynology is already adding to an already extensive body of knowledge of Pleistocene arctic floras.

References

Chaney, R. W. 1940. Tertiary forests and continental history. Bull. Geol. Soc. Amer. **51**: 469-488.

——— **and H. L. Mason.** 1936. A Pleistocene flora from Fairbanks, Alaska. Amer. Mus. Novit. No. **887.**

Heer, O. 1871. Die diluvialen Ablagerungen Spitzbergens. (*In* Die miocene Flora und Fauna Spitzbergens, pp. 80-92.) Flora Fossilis Arctica **2(3).**

———. 1878. De miocene Flora des Grinnell-Landes. Flora Fossilis Arctica **5(1).**

Lindquist, B. 1947. Two species of Betula from the Iceland Miocene. Svensk. Bot. Tidskr. **41**: 339-353.

Matthews, J. R. 1955. Origin and Distribution of the British Flora. London.

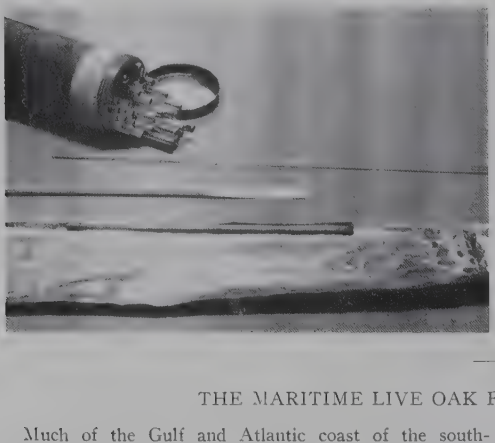
Reid, C. 1899. The Origin of the British Flora. London.

Chester A. Arnold

University of Michigan
Ann Arbor, Michigan

INCREMENT BORING CONTAINERS

The problem of handling large numbers of increment borings from trees has been variously solved by using grooved wood slabs, corrugated cardboard, and metal tubes, but the following containers have proven to the writer to be the cheapest, lightest, most convenient, and minimal of space of any.



The container tubes are made from the heaviest weight aluminum foil for wrapping frozen food. The tubes are rolled around a piece of glass tubing or rod slightly larger than the increment borings (Fig. 1). Starting at one end of the sheet of foil, roll up the tube to about four thicknesses and cut off with a razor blade. Slip out the glass tubing and fold over one end of the tube. The other end is left open to insert the increment boring and crystals of paradichlorobenzene, if desired. After inserting the boring, the upper end can be easily flattened and the code number of the specimen written on the surface of the foil with a pencil or ball-point pen. Being a permanent impression there is no danger of the marking rubbing off. The flattened end can be folded over for greater protection against moisture loss. The tubes are carried in the field in a shellacked mailing tube with screw cover.

Loren D. Potter, Chmn.

Biology Dept.
University of New Mexico
Albuquerque, New Mexico

THE MARITIME LIVE OAK FOREST IN NORTH CAROLINA

Much of the Gulf and Atlantic coast of the southeastern United States is bordered by a sand strand grading inland from bare beach to dunes of varying height and extent and supporting very similar zones of vegetation throughout. Wherever these dunes have long been relatively stable there is forest in which live oak (*Quercus virginiana*)[1] is a major component. Approaching its northern limit in North Carolina, live oak is practically restricted to a narrow fringe along the coast, less than a mile wide, and to the off-shore banks. Here it may assume complete dominance and form the evergreen maritime forest which Wells (1939) termed salt spray climax.

That salt-spray is a primary selective factor determining the species and their zonation in this environment has been amply demonstrated (Wells and Shunk, 1938; Oosting and Billings, 1942; Boyce, 1954). Unquestionably, live oak is the dominant tree in this maritime forest because the normal components of the oak-hickory association are excluded by their intolerance to salt-spray. Inland, beyond the spray zone, live oak is never dominant, presumably because it cannot compete successfully there. It is not, however, the most spray-resistant species. On the seaward side of the strand there is usually a definite zonation with sea oats (*Uniola paniculata*) occupying the foredune and other exposed places. Then follows a shrub zone with wax myrtle (*Myrica cerifera*) and yaupon (*Ilex vomitoria*) predominating, and, finally, the tree zone in which live oak is dominant.

The maritime forest must have covered extensive

[1] Nomenclature after Gray's Manual, 8th ed. 1950, or for strictly southern species, Small's Manual of the Southeastern Flora, 1933.

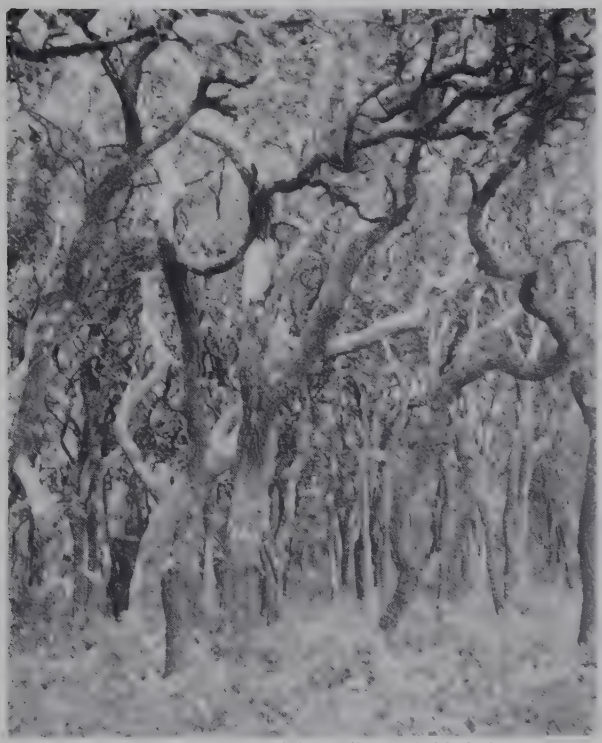


Fig. 1. Live oak stand immediately behind the yaupon-myrtle zone. Surf City, North Carolina.

areas along the North Carolina coast in the past but fire, burial by wandering dunes, or bulldozing and levelling for real estate development have eliminated all but a few relics which usually are disturbed to some degree. The best-preserved stands, briefly described by Wells (1939), are on Smith Island at the mouth of the Cape Fear River. Although the general nature of the forest is known from descriptions by several authors (Oosting, 1954) there has been no detailed study of its structure. Because the rate of its destruction by man is accelerating and complete elimination of all truly representative stands appears inevitable, it seems desirable to record the results of sociological analyses made of a number of examples studied on the outer banks and on the mainland.

Field assistance by Mr. K. O. Peck and financing by the Duke University Research Council are gratefully acknowledged.

Methods

Most of the reasonably accessible parts of the North Carolina coast were visited in search of live oak communities. Any mature stand, free of major recent disturbance, was included in the study. The most suitable stands were found on Smith Island and in areas only recently opened to real estate development (Surf City, Longbeach). Parts of these latter stands were already surveyed for building lots. One excellent small stand was on Lennox Point, Beaufort, and one near Atlantic Beach. Data were also obtained for a partially bulldozed stand on the Isle of Palms near Charleston, South Carolina.

Presence lists were made in 17 stands and those which were extensive enough (5) were analyzed by plot sampling. An area, 60 × 100 m., was roughly delimited and divided into six 10 × 100 m. strips. Two of these strips were randomly selected and each was subdivided into ten quadrats, 10 m. square. Five alternate quadrats per strip were used in sampling. Thus ten 10 × 10 m. quadrats were taken per stand. All woody plants, 1 in. d.b.h. or more, were tallied by diameters. Percentage cover was estimated for woody species less than 1 in. (2.54 cm.) d.b.h. and for herbs, in 4 × 4 m. plots nested in a fixed corner of each 10 × 10 m. plot. Species observed outside the plots were included in the presence list.

Soil profiles were observed in pits or tube samples. Representative samples were taken at various depths for the determination of texture by dry-sieving, wilting percentage, moisture equivalent, pH, calcium carbonate, organic matter, nitrogen, phosphorus, potassium and calcium. The latter five determinations were made by the Soil Testing Division of the North Carolina State Department of Agriculture, whose cooperation is gratefully acknowledged.

Results

Vegetation

The live oak trees located closest to the ocean, just behind the shrub zone, were small in height and diameter, of poor form, and of slow growth (Fig. 1). As many as 120 growth rings were common in trees less than 5 in. (12.7 cm.) d.b.h. Tree size increased landward. In its best development, on Smith Island, the forest had an average height of 55-60 ft. (16.7-18.3 m.). The top of the canopy formed an almost continuous, smooth surface,

caused by the shearing effect of wind and salt spray (Fig. 2). Live oaks 3 to 4 ft. (91-122 cm.) d.b.h. were common (the largest observed, 5 ft. 8 in. (173 cm.) d.b.h. They were widely spaced, often branching at 4 to 10 ft. (1.2-3 m.) above ground, and forming crowns as wide as the total height of the tree. *Juniperus virginiana* and an occasional *Sabal palmetto* reached into the upper story.

FIG. 2. Live oak stand, southern part of Smith Island, North Carolina. Note shearing effect of wind and salt spray on forest canopy.

A number of large red cedars were felled 30 or more years ago but most of them were abandoned on the ground. *Pinus taeda* occurred in areas that had been disturbed in the past and that were relatively sheltered from salt spray.

The understory and shrub layers were very dense, with *Ilex vomitoria, Persea borbonia, Osmanthus americanus,* and *Laurocerasus caroliniana* as the main components. *Cornus florida* was locally present; the largest ones had recently been cut. Abundant vines were *Berchemia scandens* and *Smilax* spp. (mostly *S. bona-nox*). The herb layer was sparse, except below openings in the canopy. It included mostly woody seedlings, poison ivy and a few herbaceous species. A ½ to 1-inch (1.3-2.5 cm.) dry litter, largely tough, slow-decaying, live oak leaves, covered the ground at the time of the study (June 1953).

On the southern shore of Smith Island, the fully-developed live oak forest was found directly behind dunes which were as high as the trees. Sand, blowing inland, had covered the transitional shrub zone as well as part of the forest. The landward movement of unstable coastal dunes is a normal phenomenon. Here it has been recently accentuated because records of the Army Corps of Engineers indicate that 150 years ago the forest was much closer to the ocean. A contributing cause may be the widening of the beach consequent to shoal formation by ocean currents after a dam was built upstream on the Cape Fear River (B. W. Wells, pers. comm.). Also, after cattle were introduced in 1901, the grassy, stabilized foredunes were periodically burned to provide green forage. Thus, blow-out increased as did the area of exposed beach, and dune formation and movement progressed accordingly.

In contrast, along the eastern shore of Smith Island, the shrub zone extended to the beach from which it was separated by an almost vertical, 4-5 foot (1.2-1.5 m.) wall of sand. Here the ocean is encroaching on the land, as evidenced by palmetto snags still standing on what is now the beach. This is in line with the general subsidence of the Atlantic shoreline (Marmer, 1951).

The live-oak stands observed elsewhere on the banks or on the mainland were all located behind a shrub zone with which they formed a continuous ecotone. Inland, they eventually merged with stands of turkey oak (*Quercus laevis*) and other scrub oaks, and loblolly pine.

Floristic Composition.—The species list, covering 17 stands, included 107 phanerogams (28 trees, 21 shrubs and vines, and 58 herbs). Presence percentages for the most important tree species are given in Table I. Other trees and shrubs were, in order of decreasing presence, *Carya* spp. (41%), *Diospyros virginiana, Nyssa sylvatica* v. *biflora, Ilex coriacea, Sassafras albidum, Clethra alnifolia, Magnolia virginiana, Rhus copallina, Pyrus arbutifolia, Lyonia lucida, Quercus phellos, Prunus serotina, Quercus marilandica, Q. falcata, Pinus australis,* and *Liquidambar styraciflua* (6%).

TABLE I. Density of seedlings (1 inch diameter and less), basal area, and presence of the main woody species of the live oak forest

Species	Seedlings per acre (average of 5 stands)	Basal area (average of 5 stands) as % of total	Presence % (over 17 stands)
Quercus virginiana	1136	62.0	100
Persea borbonia	469	8.5	82
Carpinus caroliniana	152	5.5	12
Juniperus virginiana	135	4.4	100
Pinus taeda	5	3.7	53
Ilex vomitoria	∞	3.2	88
Osmanthus americanus	39	2.7	82
Ilex opaca	53	2.1	65
Sabal palmetto	0	1.7	35
Cornus florida	152	1.6	24
Laurocerasus caroliniana	530	1.6	47
Morus rubra	12	1.4	24
Quercus nigra	30	<1.0	65
Callicarpa americana	182	"	71
Persea borbonia f. *pubescens*	92	"	59
Nyssa sylvatica	1	"	29
Batodendron arboreum	17	"	41
Myrica cerifera	18	"	71
Aralia spinosa	6	"	29
Acer rubrum	32	"	18
Total		177.305 sq. ft./acre (40.64m.²/Ha.)	

Of the lesser vegetation, the following occurred in more than half of the stands: *Vitis rotundifolia* (100%), *Smilax* spp. (100%), *Rhus radicans* (94%), *Elephantopus nudatus* (77%), *Mitchella repens* (65%), *Parthenocissus quinquefolia* (65%), *Bignonia capreolata* (62%), and *Asplenium platyneuron* (50%). Species present in at least three but less than nine stands, were, in order of decreasing importance: *Ascyrum hypericoides, Gelsemium sempervirens, Panicum* spp., *Galium pilosum, Berchemia scandens, Galactia macreei, Passiflora lutea, Desmodium* spp., *Amorpha fruticosa, Vaccinium stamineum, Rhynchospora* sp., *Pteridium aquilinum, Erythrina herbacea, Ampelopsis arborea, Campsis radicans, Arundinaria* spp., and *Euphorbia ipecacuanhae.*

Location of stands and presence or absence of species had little or no relationship except that *Persea borbonia* f. *pubescens* and *Nyssa* did not occur in stands on Smith Island but *Sabal palmetto, Cornus florida,* and *Rhynchospora* sp., present in these stands, were generally absent

TABLE II. Physical and chemical characteristics of representative samples of coastal soils in the three vegetational zones

Vegetational zone	Average sample depth (inches)	TEXTURE (international classification)			Organic matter %	Moisture equivalent %	Wilting percentage	pH	N %	P ppm	K m.e./100 gm.	Ca m.e./100 gm.	$CaCO_3$ %
		Coarse sand %	Fine sand %	Fines (<.05 mm) %									
Uniola dune..	6	41.3	58.6	.1	.8	2.57	.58	6.5	.025	140	.03	8.0	1.4
Shrub zone...	6	60.1	39.7	.2	.7	2.45	.60	6.0	.016	19	.03	.8	<1.0
	24	34.2	65.6	.2	.2	1.58	—	5.8	.009	5	.02	.3	<1.0
Live oak forest													
Smith I. 1	6	54.2	45.7	.1	1.0	1.80	.77	5.4	.025	4	.02	.7	<1.0
	24	40.8	59.0	.2	.4	1.44	—	5.5	.015	7	.02	1.0	<1.0
Smith I. 2	6	76.0	23.7	.3	1.9	2.29	.73	5.4	.039	70	.06	8.0	8.0
	24	84.9	15.0	.1	.2	1.55	—	6.3	.012	9	.02	8.0	8.4
Surf City....	6	32.0	67.3	.7	2.6	5.46	—	4.3	.086	14	.08	.7	<1.0
	24	18.9	80.4	.7	1.3	3.15	2.16	4.6	.034	66	.03	.1	<1.0

elsewhere. Sabal, incidentally, reaches the northern extremity of its natural range on Smith Island.

Stand Analysis.—Quantitative data on stand structure were obtained in 5 stands representing the best development of the forest. Three were located on Smith Island, one near Surf City, and one at Beaufort.

Average basal area per species for all stands and average seedling numbers are given in Table I. Of a total basal area of 177 square feet per acre (40.64 $m.^2$/Ha.), live oak contributed 62%, *Persea borbonia* only 8.5%, and the remaining 29.5% was distributed among 18 species. Live oak exceeded all species in seedling density with the exception of yaupon, seedlings and saplings of which covered as much as 20% of the total area of several sample plots. Next came *Laurocerasus caroliniana, Persea borbonia* and *Callicarpa americana.*

Distribution of stems per diameter class, above 2-inch (5.08 cm.) d.b.h., is illustrated in Figure 3. The curve

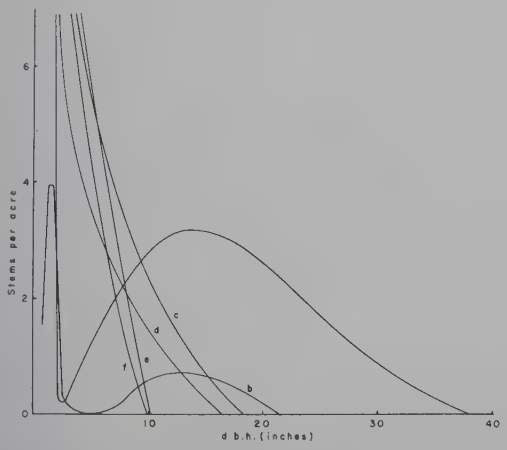


FIG. 3. Average frequency distributions, in one-inch (2.54 cm.) diameter classes, of representative species of the maritime forest. a: *Quercus virginiana;* b: *Pinus taeda;* c: *Persea borbonia;* d: *Juniperus virginiana;* e: *Osmanthus americanus;* f: *Cornus florida.* All curves are freehand drawn.

for live oak indicates that the modal tree was close to 14 inches (35.6 cm.) d.b.h. The size distribution of the live oak suggests that such stands are more or less even-aged and originated several hundred years ago. Although numerous seedlings were observed under small openings in the canopy, no saplings were noted. Viable seeds are thus produced in appreciable numbers but the canopy is probably too dense to allow survival of the seedlings for any number of years.

Secondary components of the tree layer (*Juniperus, Persea, Osmanthus, Cornus*) exhibited typical curves for uneven-aged populations, with increasingly larger frequencies in the lower diameter classes. Loblolly pine had a distribution of the same shape as that of live oak, except for the seedling class. Its occurrence was restricted to openings created in the stands, sometime in the past, possibly when some of the red cedars were logged.

The herb layer was generally of very little importance. Rarely did any single species cover more than 5% of the area of the 4 × 4 m. plots. *Rhus radicans* occupied as much as 40% of a few plots and *Elephantopus nudatus,* 15%. In the Surf City stand, however, *Mitchella repens* was abundant with up to 90% coverage in several plots.

Soils

The maritime forest has developed on sand dunes, as evidenced by the rolling topography inside the stands. Small hills alternate with depressions which, when deep enough, are marshy. Most of the sites have undoubtedly been forested for long periods of time. Geological evidence indicates that the land occupied by the forest on Smith Island was exposed by the retreating ocean at the onset of Wisconsin glaciation (B. W. Wells, pers. comm.). Yet very little profile development was observed. Under a one-inch (2.5 cm.) thick, dry litter there usually was a 1- to 2-inch (2.5-5 cm.) fermentation layer, then a zone of apparently leached, white-grey sand, of variable depth but often 10 to 12 inches (25-30 cm.) thick. The underlying sand layers varied in texture, color, and thickness. They are probably geologic strata rather than soil horizons. A brown zone, rich in shell fragments was often present. The structure was single-grained, except for very soft, brown concretions in some of the yellow sandy layers. Roots penetrated deeply in

the soil; large numbers were frequently present 5 feet (1.5 m.) below the surface. The watertable was usually within 3 feet (0.9 m.) of the bottom of the small depressions.

In the Beaufort stand, a wet, dark-brown, fine sand, relatively rich in organic matter (2%), occurred at a depth of 25 inches (64 cm.). The soil surface here was almost level. It is probable that the area was at one time a salt marsh which was buried under about 2 feet (61 cm.) of sand before the live oak became established.

Some physical and chemical properties of the forest soils are presented in Table II, together with analyses of representative soils of the shrub zone and of the foredune, in the *Uniola paniculata* zone. Texture was coarse, the amount of fine particles (smaller than 0.05 mm.) being less than 1%. Percentage of coarse and fine sand varied widely. Regardless of vegetation type, loss on ignition was generally greater in the upper 6 inches (13 cm.) than at 20-24 inches (51-61 cm.) but was only slightly higher in the forest soils than on the grassy dunes. Wilting percentages and moisture equivalents (the latter admittedly lower than field capacity in sandy soils) were low, and related to loss-on-ignition values. Nitrogen, potassium and phosporus contents were very low to low, except for high concentrations of phosphorus in dune soil and the topsoil of one stand. Calcium and calcium carbonate contents were correlated with the amounts of shell fragments. pH was slightly higher, approaching neutrality, in dune sand.

The analyses made of soils from the forested and non-forested areas indicate that this fully-developed forest, undoubtedly established for a long period of time, has very little effect on soil development in the coarse coastal sediments.

Summary

Quantitative data were obtained in 17 stands of the maritime live oak forest of North Carolina. The average basal area was found to be 177 square feet per acre with live oak contributing 62% of the total. Live oak seedlings are abundant but there are almost no saplings. The shrub layer is very dense, with *Persea, Juniperus,* and yaupon as principal species. The herb layer is sparse. Soil analyses indicate practically no profile development under the old live oak forest as compared with the grassy dunes.

References

Boyce, S. G. 1954. The salt spray community. Ecological Monog. **24**: 29-67.

Marmer, H. A. 1951. Sea level changes along the coast. Shore and Beach **19**: 22-23.

Oosting, H. J. 1954. Ecological processes and vegetation of the maritime strand in the southeastern United States. Bot. Rev. **20**: 226-262.

——— **and W. D. Billings.** 1942. Factors effecting vegetational zonation on coastal dunes. Ecology **23**: 131-142.

Wells, B. W. 1939. A new forest climax: the salt spray climax of Smith Island, N. C. Torrey Bot. Club Bull. **66**: 629-634.

——— **and I. V. Shunk.** 1938. Salt spray: an important factor in coastal ecology. Torrey Bot. Club Bull. **65**: 485-492.

Philippe F. Bourdeau
Henry J. Oosting
School of Forestry, Yale University,
New Haven, Connecticut;
Department of Botany, Duke University,
Durham, North Carolina.

A NATURALLY OCCURRING VISIBLE THERMOCLINE

Although the thermocline is a normal attribute of thermally stratified bodies of water, the writer believes this to be the first report of one being visible under natural conditions.

On July 24, 1958, the writer was skin diving with Aqualung together with a student companion, Mr. Richard Shaw, in Barber's Pond, Washington Co., R. I. Access was from a dock on the east shore. At a depth of 4-5 feet, a horizontally oriented gossamer sheet of 2-5 mm. thickness extended as far as vision was possible. The sudden change in temperature at this exact layer revealed it to be lying at the thermocline, at an unusually sharp interface between the warm, rather greenish turbid water of the epilimnion and the cool, clear brown water of the hypolimnion. On waving one's hand gently up and down at the layer, the sheet could be undulated without destroying its unity. Its distinctness increased immediately over the beds of vegetation, which consisted primarily of *Potamogeton capillaceus, Najas guadaloupensis,* and *Ceratophyllum demersum.* This seemed to be consistent with the greater turbidity noted over vegetation, suggesting an effect by vegetation in augmenting flocculating conditions in the epilimnion. The layer was seen on succeeding dives of August 3, 5, 9, and 12. It dropped at an irregular rate to approximately 10 feet by August 12, and had become diffused to approximately 20 cm. thick. Within this thicker layer numerous groups of thin laminae were noticeable. By August 20, it had reached the bottom in the area being studied, and therefore was no longer apparent. It had lasted somewhat less than a month, no evidence of the condition having been noted on July 17.

A sharp change in temperature was experienced on passing through the thermocline. Measurements of temperature made on August 3, taken just (2-5 cm.) above the flocculent layer read 79°F, whereas 3-5 cm. below a reading of 65°F was found.

A sharp reduction in light intensity was observed, an impressive diminution of light being experienced on descending through the visible thermocline. A crude measurement of light intensity was made by taking a maximum reading on the palm of the hand by a Fenjohn deep-water photographic light meter. Readings were obtained of 18 (ca. 75 foot candles) Weston units above and 9 (ca. 15 ft. cd.) units below the thermocline, representing a reduction of about 80 per cent in light.

Barber's Pond was described by Saila and Horton (1957).[1] It is a small body of water, approximately 2000 feet long, averaging about 12 feet deep with a maximum depth of 18 feet, having soft, neutral to mildly acid water, with a strong brown color due to bog runoff.

Investigations of the flocculent material and conditions inducing the formation of the visible layer are anticipated.

R. D. Wood
Department of Botany
University of Rhode Island
Kingston, Rhode Island

[1] Saila, S. B., and D. Horton. 1957. Fisheries investigation and management in Rhode Island lakes and ponds. 134 pp. Fisheries Publ. No. 3, available from R. I. Dept. Agric. and Conserv., Div. of Fish and Game, Providence, R. I.

COMMENTS ON "PLANT ECOLOGY AS A BRANCH OF BOTANY"

Major (1958), in a generally excellent and thought-provoking article writes, ". . . plant geography is certainly one field where causation does not apply." This statement would be greatly improved by altering "does not" to "does, in complex fashion." Is it to be expected that with three major variables: climate, physiography and parent material, environment should bear a "clear one-to-one relationship" to vegetation? But if the situation is complex, this is no sufficient reason to throw out the possibility of elucidating causality in the intricate web of plant-environment relations. In the present state of ecological knowledge, an algebraic treatment of the environmental complex (Major, 1951) is only an elegant form of begging the question, and its ultimate usefulness awaits further developments resulting from application of the logic of causation, which is rejected by Major (1958, p. 360).

Major states further: "In summary there are two differences between ecology and plant geography: (1) A theoretical difference, since plant geography is concerned with the relations of plants to the earth and not to environment as such and (2) A practical difference, since the relative scale of study usually differs, partly, at least, as a consequence of the first point." His ratio: ecology is to plant geography as 10 is to 100.

If we narrow his usage of the term plant geography to the floristic, or chorological division of that field of study, statement (1) is at least partly true. But it is evident that he gives plant geography its usual wide scope, including both floristic and physiognomic studies. In this broad sense, plant geography is, or should be, very much concerned with the relation of vegetation to environment, from the standpoint of adaptive, or at least comparative, morphology and physiology. Major himself later contradicts statement (1) when he writes (p. 360) ". . . plant geography . . . includes the study of plants in relation to environment."

Statement (2) assigns a relatively small scale to ecology compared to plant geography. If we allow that macroclimate is indeed one of the most important of ecological factors, then ecology has expanded to the scale of plant geography; and if we admit narrow endemism as an important aspect of plant geography, then this discipline includes also the scale of Major's ecology, which is apparently restricted to the local level of microclimatic, physiographic and parent material effects.

Other arguments can be adduced to question the wisdom of a segregation of plant ecology and plant geography as separate disciplines. Plant ecology is a point of view (ultimately physiological) and as such, requires subject matter to become a field of study. That subject matter is vegetation, and the field of study is plant geography on a physiological basis. The scope of this study is local when it deals with the relation of vegetation to substratum and microclimate, and global when it deals with the relation of vegetation to macroclimae.

On the other hand, floristic plant geography or plant chorology, which is concerned with the problem of geographical distribution per se, certainly constitutes a different point of view from ecology. It is advantageously segregated from physiological plant geography and merged with zoogeography, which is also concerned with chorology, routes of migration, refugia, etc. This merger has existed at least since Wallace (1880).

References

Major, J. 1951. A functional, factorial approach to plant ecology. Ecology **32**: 392-412.

Major, J. 1958. Plant ecology as a branch of botany. Ecology **39**: 352-363.

Wallace, A. R. 1880. Island life. 526 pp. Macmillan: London.

Philip V. Wells

Department of Botany
Duke University
Durham, North Carolina

ISOTHERMAL CONDITIONS IN TROPICAL SOIL

One of the impressive features of tropical forested areas is the uniformity of meteorological conditions. Temperatures of the soil under tropical rainforest are perhaps the most uniform of any land surface area. Richards (1952 p. 138) quotes Mohr and Bernard records of temperatures of the soil under forest at sea level in Indonesia (Netherlands Indies) as 25-27° C and at a depth of a meter "it is quite constant; even at 60 cm it is essentially constant. At Yangambi in the Belgian Congo the mean temperature of the soil at 50 cm below the surface is 26.2° and the annual range 1.5°; at a depth of 50-75 cm all traces of a diurnal variation of temperature disappear."

Temperatures taken by the writer in 1948 on the Central African Expedition of the American Museum of Natural History agree in general with those above although taken with unstandardized thermometers and tenths were estimated. For example, 10 miles east of Stanleyville, Belgian Congo the leaf cover of the soil under rain forest on March 17 was 26.4°, under this it was 25.3°, at a depth of about 3 cm, 24.4° and at a depth of 13 cm, about 23.5° C. The Lualaba River here the next day was 26° C in swift current within 10 cm of the surface. During March 15 three rivers of the Congo system that were crossed by ferry had temperatues in the swift current within 10 cm of the surface of 27° (Aruwimi R., after a heavy morning rain, 2:20 p.m.), 26.7° (Lindi R., 4:20 p.m.) and 26.1° (Tshopo R., 5:30 p.m.), the first river being much the largest and the last much the smallest. Since all flowed through forest of high trees forming vertical walls, insolation was reduced and water temperature should reflect the soil temperature fairly closely.

It is the purpose of this note to record temperatures taken at exactly the same 2 sites at 3 times of the year on Barro Colorado Island, Panama Canal Zone. The temperatures were needed for duplicating conditions in the laboratory for ant colonies. One of the sites chosen had a large colony of the leaf-cutting ant, *Atta colombica tonsipes* Santschi, and was in red clay in typical forest shade 4-5 meters from the edge of the laboratory clearing. The presence of the ants had no bearing on the temperatures. The other site, also in red clay, was in the laboratory clearing with full insolation and had at first a young colony of this species that was removed for study in June 1955. Representative air temperature and relative humidity graphs for the same clearing and for a forest site here in 1938 were published by Park, Barden

and Williams (1940 pp. 128-129). The forest site showed the relative humidity almost constant (92-98%, most hours 96-98%) and air temperatures of 24-26.5° C for a week in July.

Temperatures in Groups I and II of Table I were taken with the same thermometers which read consistently the same and had been calibrated with accurate thermometers. They were English laboratory thermometers (T & M Ltd, Gold E, Mercury, 297 mm x 5 mm). One of these was used for Group III and was supplemented by others of similar type; in all cases tenths were estimated. Sub-surface readings were taken by digging a hole sufficiently large to hold the thermometer horizontal; it was then thrust into the soil so that the bulb and adjacent few centimeters were embedded and readings were taken *in situ* after several minutes when the column became stable. For surface temperatures the mercury bulb was placed loosely on the soil with the instrument horizontal. Air temperatures were taken with the thermometer fully exposed and, of course, fluctuating with intermittent clouds and breezes in the clearing.

The extreme constancy of sub-surface temperatures in forested areas is indicated by the right-hand columns in the three groups, all made at the same site but in March, June and December. These showed no significant variation. June and December surface temperatures were also the same but that of March (at the end of a severe dry season) reflected the high insolation (more sunny hours) and air temperatures, which had a cumulative effect. In March more spots of sunlight occurred here for more hours of the day.

At the same open site of the laboratory clearing the highest subsurface temperatures were similarly in March. Those of June and December, while consistently higher than in the shade, are variable and reflect daily differences in amount of cloud cover or the accumulation of such differences; the December day was towards the end of a rainy season. The highest air and surface temperatures then merely reflect a sunny period and doubtless could be duplicated or exceeded during the dry season.

Other Barro Colorado Island Temperatures

In connection with research on fungus-growing ants, temperatures at other naturally shaded sites were taken. About 100 meters distant from the shaded site of Table I, where a large nest of *Atta colombica tonsipes* occurs, the air temperature at a height of one meter on 16 July 1954 was 26.2° C at 10:15 a.m., on the soil surface it was 25.3° and about 20 cm down one of the tunnels of the ants it was 24.3° C. The latter temperature is unusually low and may represent the cooling effect of a current of air. At another shaded nest of this ant (near Donato No. 4 of the trails) the temperature one meter above ground was 27.5° C, at 2:30 p.m. on 16 July 1954; the surface was 27.0° and at a depth of about 30 cm it was 25.5°. By 3:10 p.m. the surface was 26° and at 1.5 cm above the soil it was 26.8°. The surface temperature at 11:00 a.m. here, but on 28 March 1957, was 27.6° and it was the same down one of the tunnels at a depth of 20 cm.

TABLE I. Temperatures in °C at open and at shaded sites on Barro Colorado Island, Panama Canal Zone

	GROUP I		GROUP II		GROUP III	
Date...	20 June, 1955		27 March, 1957		22 December, 1957	
	Open Site	Shaded Site	Open Site	Shaded Site	Open Site	Shaded Site
Time...	3:30-40 pm	3:45-55 pm	3:30-40 pm	3:45-55 pm	3:10-25 pm	3:30-40 pm
1 meter in air...	26.6	26.3	29.8-30.0	27.8	31.0-32.0	27.5-29.0
Surface of soil...	28.2	26.5	36.8-39.4	27.8	39.0-40.9	26.6
Depth 10 cm...	30.8	26.2	32.9	26.1	30.2	26.0
Depth 20 cm...	30.3	26.0	32.0	25.7	29.0	25.7
Depth 30 cm...	29.4	26.0	32.2	25.7	28.6	26.0

The indications are that the fungus-growing habit in ants originated in some such tropical rainforest area. The above range of temperatures, when duplicated in the laboratory, have proven satisfactory for maintaining a considerable variety of species and artificial cultures of their fungi.

SUMMARY

A comparison of sub-surface temperatures at a forest and at a clearing site on Barro Colorado Island, Canal Zone was made at 3 times of the year. At depths of 10, 20 and 30 cm at the forest site in March, June and December conditions were isothermal (26° ± 0.3°). In the clearing at the same depths and time the range was 28.6-30.8°C. These are compared with other subsurface rain forest temperatures of 23.5-27.6°C here and in Africa, and they indicate relative constancy when compared with non-tropical areas.

REFERENCES

Park, O., Barden, A. and Williams, E. 1940. Studies in nocturnal ecology, IX. Further analysis of activity of Panama rain forest animals. Ecology, **21**: 122-134.

Richards, P. W. 1952. The tropical rain forest. Cambridge (England), University Press.

NEAL A. WEBER

SWARTHMORE COLLEGE
SWARTHMORE, PENNSYLVANIA

HIGH INCIDENCE OF VERTEBRAL DEFORMITIES IN TWO NATURAL POPULATIONS OF FISHES INHABITING WARM SPRINGS[1]

Laboratory-reared fishes have been shown to have vertebral anomalies. High incidence has been correlated with a number of unfavorable conditions, including constant and unfavorable high temperature during ontogeny (Mottley 1937, Gabriel 1944). Concentrations of dissolved solids and gases may also cause abnormalities. In fact abnormalities correlated with high temperature may actually be caused in part by the concentrations of oxygen and/or carbon dioxide in solution at these temperatures.

Two collections (Texas Natural History Collection

[1] The author wishes to acknowledge the assistance of Mr. Harold Broderick of the U. S. National Park Service, Dr. W. W. Milstead then on the faculty of Sul Ross State College, and the many others who assisted in the field work. National Science Foundation Grant 2214 supported my field work.

Nos. 5314 and 5650) of the common mosquito fish, *Gambusia affinis* (Baird and Girard), contain many specimens with vertebral deformities. Each of the 38 specimens comprising TNHC 5314 has an abnormal vertebral column, although only 28 are strongly malformed. Forty-six of the 73 specimens comprising TNHC 5650 have abnormal vertebral columns, although only 35 are strongly malformed. In extreme examples the vertebral colum is exceedingly serpentine, with scarcely any straight segment. Many of the fins are also malformed; however, all are present and their counts approximate those of nearby populations. Likewise scale patterns are distorted but the number in a longitudinal series approximates that of nearby populations. The deformities and adverse environmental factors did not prevent reproduction, as pregnant females and young occurred there. Significant differences in meristic characters might be expected as these are generally known to be thermally plastic and related species have been shown to have their counts changed by temperatures during ontogeny (Hubbs and Springer 1957). However, Tåning (1952) has shown that extreme temperatures can give similar meristic counts.

The fishes comprising TNHC 5314 were collected on October 9, 1956, from the Graham Ranch Warm Spring, one miles southwest of the Boquillas Ranger Station in the Big Bend National Park, Texas. All of the fish came from a stone-lined spring pool which is drained by a pipe from which the water falls one foot to the lower pools. Temperatures do not vary significantly from place to place in the spring pool. On the collection date the temperature was 34.8°C and on April 27, 1956 it was 34.5°C. Mosquito fish have recently been introduced into the spring pool as none were observed there in two visits in June, 1954. Moreover, Hubbs and Springer (1957) believe that the common mosquito fish recently has been introduced into this semi-isolated spring system. One adult blue catfish, *Ictalurus furcatus* (Le Sueur), was the only other fish taken with the mosquito fish.

The fishes comprising TNHC 5650 were collected on August 15, 1957, from the "bathtub spring" three-quarters of a mile southwest of Boquillas village, Coahuila, Mexico. The locality is approximately 400 yards east of the Graham Ranch Warm Springs, and thus probably from the same aquifer. The fish were collected from the spring pool and adjacent irrigation ditch. The temperature varied between 35°C and 35.5°C. Rio Grande fishes can often enter this irrigation system and gain access to the spring pool. Young *Carpioides carpio* (Rafinesque) were the only other fish found in the spring. As more than half of the non-deformed mosquito fish were males, it is likely that immigrants contribute to the spring population. Hildebrand (1927) and others have shown that female numbers far exceed those of males in natural populations. Moreover, my unpublished studies on other *Gambusia* populations have shown that males are far more likely to stray than are females.

The 2 warm spring populations have similar ecologic conditions and a similar frequency of vertebral abnormalities. It is possible that they differ from adjacent waters in 2 ecologic conditions (water chemistry and consistently high temperature) which may cause the abnormalities. Chemical causes (other than dissolved gases that may be correlated with high temperature) are doubtful because the cooler main pool at Graham Ranch, which receives its water from the spring pool, has normal fish. Moreover, non-deformed mosquito fish have been taken in waters with a great variety of dissolved solids. Predator selection may play a role, as one habitat had no visible potential predators, and the other contained only one large bottom inhabiting catfish that would not likely consume many surface inhabiting mosquito fish. (Canibalism, however, does occur and it might eventually lower the percentage of deformed fish.)

Constant high temperature rather than occasional hot water is suspected as the cause of the high incidence of deformities. Non-deformed common mosquito fish often have been collected in waters warmer than 35°C and occasionally as high as 39.5°C. These habitats, however, have great seasonal thermal fluctuations. The highest incidence of major vertebral abnormalities found in any other natural population of mosquito fish is 4%. This collection, from Cameron County, Texas, is from a habitat that has high summer temperatures. Vertebral deformities must occur occasionally from fish exposed to high temperatures during ontogeny in summer. Perhaps the concentration of vertebral abnormalities in percid fishes from Oklahoma, Kansas, and Mexico, mentioned by Bailey and Gosline (1955) is due to high summer temperatures in these areas.

Other fishes can withstand constant higher temperatures; for example Miller (1948) reported *Cyprinodon* abundant in constant thermal waters up to 37°C and rarely to 40°C but did not mention deformities. Jordan and Richardson (1907) reported *Cyprinodon* in waters of 48.9°C but it is not certain that the fish were in that specific temperature.

References

Bailey, R. M., and W. A. Gosline. 1955. Variation and systematic significance of vertebral counts in the American fishes of the family Percidae. Misc. Pub. Mus. Zool. Univ. Mich., 93.

Gabriel, M. L. Factors affecting the number and form of vertebrae in Fundulus heteroclitus. J. Exp. Zool., **95**: 105-147.

Hildebrand, S. F. 1927. Sex ratio in *Gambusia*. Biol. Bull., **53**: 390-404.

Hubbs, Clark, and V. G. Springer. 1957. A revision of the *Gambusia nobilis* species group, with descriptions of three new species, and notes on their variation, ecology, and evolution. Texas J. Sci., **9**: 279-327.

Jordan, D. S., and R. E. Richardson. 1907. Description of a new species of killifish, *Lucania browni*, from a hot spring in Lower California. Proc. U. S. Nat. Mus., **33**: 319-321.

Miller, R. R. 1948. The cyprinodont fishes of the Death Valley System of eastern California and southwestern Nevada. Misc. Pub. Mus. Zool. Univ. Mich., 68.

Mottley, C. McC. 1937. The number of vertebrae in trout (*Salmo*). J. Biol. Bd. Can., **3**: 169-176.

Tåning, Å. Vedel. 1952. Experimental study of meristic characters in fishes. Biol. Rev., **27**: 169-193.

Clark Hubbs

Department of Zoology
The University of Texas
Austin, Texas

EOSINOPHIL RESPONSE OF C57BR MICE TO BEHAVIORAL DISTURBANCE[1]

The number of circulating eosinophils is known to be a sensitive index of systemic stress in various experimental animals. A stress of relatively short duration produces a temporary eosinopenia, in which the eosinophil count reaches its lowest level approximately 4 hours after the onset of stress, followed by a temporary eosinophilia 8 to 10 hours after the onset of stress (Speirs and Meyer 1949). A prolonged stress apparently produces a prolonged reduction in circulating eosinophils, at least with low temperature as the stressor agent (Louch, Meyer, and Emlen 1953). The decline in eosinophils following stress is generally interpreted as a response to increased levels of cortical steroids in the blood. This response is sufficiently constant in experimental animals to provide a bioassay method for cortisone (Dumm and Ralli 1954).

Most of the previous work on stress and eosinophil level has employed physical factors such as cold, venesection, and injection of foreign substances as stressor agent (Louch, Meyer, and Emlen 1953, Halberg 1953, Denison and Zarrow 1954). Dreyfuss and Feldman (1952) have shown that the number of circulating eosinophils in the human responds to behavioral stress, but this field is relatively untouched in animal experimentation. This report describes the effect of 3 types of short-term behavioral disturbance on the eosinophil count of C57BR mice.

Methods

Forty male mice, 4 to 5 weeks of age (10-15 grams) were isolated in individual cages for a 3-week period. The mice were of the C57 brown strain (C57BR/cd JAX) obtained from the Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine. Food and water were supplied *ad lib.* and each cage (7 x 9½ x 7 inches) was provided with a small handful of shredded paper as nesting cover. Temperature was maintained at 70° to 75° F and artificial light was provided from 7 a.m. until 10 p.m. At the end of the 3-week isolation period, blood counts were taken on each mouse at 4-day intervals for 16 days. The animals were handled on a rotation schedule so that 10 individuals were sampled each day. This experimental pattern was chosen to insure complete recovery of each individual from any stress associated with blood sampling. The animals averaged 23 grams in body weight when the blood counts were started.

From the 5th through the 12th day of the experiment, 32 mice were subjected to experimental treatment daily from 9 a.m. until 10 a.m. Eight mice remained as undisturbed controls.

Three types of experimental treatment were utilized, designed to provide different degrees of behavioral disturbance. Mice of experimental group A (8 individuals) were picked up at 9 a.m., handled gently for a few seconds and returned to the same cage. The handling was repeated at 10 a.m. Mice of experimental group B (8 individuals) were picked up at 9 a.m. and placed in another cage previously occupied by another male mouse. The cages were identical. At 10 a.m. all mice were returned to their original cages. Mice of experimental group C (16 individuals) were picked up at 9 a.m. and placed in a larger cage (16 x 9½ x 7 inches) in groups of 4. Larger cages were used to permit greater movement and interactions of the mice. They remained in this grouping for one hour, and then all were returned to their original cages.

Eosinophil counts were made from 1 p.m. to 3 p.m. This period was chosen to coincide with the time of greatest eosinopenia. Direct eosinophil counts were made following the technique of Speirs and Meyer (1949). Fuchs-Rosenthal counting chambers of 0.2 mm depth were utilized.

Results and Discussion

Figure 1 shows the results of this experiment. These data, given in eosinophils per chamber, may be converted to eosinophils per cubic millimeter of blood by multiplying by 6.25. Each dot on the graph represents the average of counts from 4 mice, except the data of experimental group C which represent the average of 8 mice. The sample sizes were necessarily limited by the strict time regimen of the sampling.

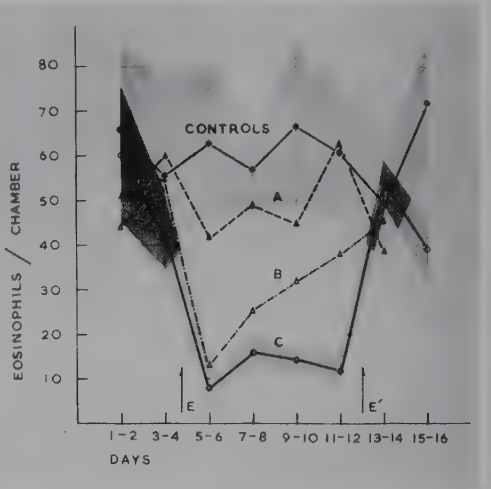


Fig. 1. Direct eosinophil counts of C57BR mice taken from 1 p.m. to 3 p.m. Experimental groups A, B, and C subjected to varying degrees of behavioral stress from 9 a.m. to 10 a.m., days 5 (E) through 12 (E'). See text for description of stress treatments. Shaded areas represent standard errors of counts for control animals and group C.

Experimental group C (mice which were placed in groups of 4) showed a marked eosinopenia throughout the 8 days of the stress treatment. The eosinophil count of these mice averaged 80% lower than that of the controls. These animals fought sporadically during their hour of social contact, but they were not openly wounded.

Experimental group B (mice placed in a different cage, but remaining isolated) revealed a marked eosinopenia the first 2 days of the treatment, but apparently adjustment to this new situation occurred, for the eosinophil count returned to normal levels. Experimental group A (mice which were merely handled) showed a very minor and nonsignificant eosinopenia.

The patterns of experimental groups A and B are particularly interesting. Group A demonstrates that handling *per se* was not a significant stress experience in this

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experiment. The initial marked eosinophil response of group B suggests that the new surrroundings elicited a stress response almost as great as actual contact and fighting with strange males. The new cage, into which each mouse was placed, differed most notably from the original cage in possessing the odor of a strange mouse. All other physical factors, such as food, water, cover, and space were as nearly identical as possible.

If further work continues to demonstrate this phenomenon in mice and other animals, it would have widespread significance in several aspects of animal behavior and sociobiology. It would suggest, for example, that the displacement of an animal into a strange habitat may be a stressful experience even though the habitat is adequate in all physical features. One would expect that sensitive hormonal responses such as this would be particularly important in species showing strong territorial behavior. In such animals, a variety of social factors (including alterations of population density, spatial relationships, dispersal movements, activity patterns and dominance relationships) might readily produce endocrine changes and be reflected in changed eosinophil levels. Such a change has been demonstrated by Louch (1958) in natural populations of voles (*Microtus pennsylvanicus*) of different densities. The work of Louch indicates that the eosinophil count can be used in certain situations as one index to the physiological condition of natural populations.

Summary

Young adult male mice were subjected to 3 different types of short-term behavioral disturbance daily from 9 a.m. to 10 a.m. Direct eosinophil counts taken 4 hours later revealed: (1) placing isolated males in groups of 4 (group C) produced an 80% decline in circulating eosinophils for each of 8 days of experimental trials, (2) placing isolated males in strange cages (group B) produced a 75% decline for 2 days, but the counts gradually returned to normal by the eighth day, (3) handling of the mice *per se* (group A) did not produce a significant change in eosinophil levels.

References

Denison, M. E. and M. X. Zarrow. 1954. Eosinophils of blood during prolonged exposure to cold and chronic administration of cortisone acetate. Proc. Soc. Exp. Biol. and Med. **85**: 433-437.

Dreyfuss, F. and S. Feldman. 1952. Eosinopenia induced by emotional states. Acta med. Scandinav. **144**: 107-113.

Dumm, M. E. and E. P. Ralli. 1954. A critical analysis of the eosinophile response in rats to ACTH and cortisone. Endocrin. **54**: 71-80.

Halberg, F. 1953. Changes in eosinophil count of mice with venesections repeated at intervals of several days. Proc. Soc. Exp. Biol. and Med. **82**: 160-162.

Louch, C. D. 1958. Adrenocortical activity in two meadow vole populations. Jour. Mamm. **39**: 109-116.

———, **R. K. Meyer and J. T. Emlen.** 1953. Effect of stress on diurnal fluctuations in eosinophils of the laboratory mouse. Proc. Soc. Exp. Biol. and Med. **82**: 668-671.

Speirs, R. S. and R. K. Meyer. 1949. The effect of stress, adrenal and adrenocorticotrophic hormones on the circulating eosinophils of mice. Endocrin. **45**: 403-429.

Charles H. Southwick

Department of Zoology
Ohio University
Athens, Ohio

CIRCUMSTANTIAL EVIDENCE INDICATING A POPULATION SHIFT OF THE LIZARD *LYGOSOMA*, IN EASTERN MISSOURI

Odum (1953: 125) has stated that ". . . data on population growth of field populations are few, incomplete, and hard to come by." Comparisons of present populations with annotations in early faunal surveys are often the only means of evaluating recent growth or decline of populations, albeit the results are crude and subjective.

The Ground Skink, *Lygosoma laterale* (= *Leiolopisma unicolor*), is an "abundant" species in St. Louis County, Missouri. It can be observed in almost any wooded area, especially in hilly sections. Turning rocks will usually reveal many more individuals than would otherwise be seen. Its apparent abundance has been estimated as second only to *Sceloporus*, at a locality 40 miles southwestward of St. Louis (Myers 1957: 290).

From the writings of Julius Hurter, however, *Lygosoma* appears to have been scarce around the turn of the century. Hurter, a resident of St. Louis, collected birds and later, amphibians and reptiles in the region from about 1866 to 1915. He was a competent and thorough collector, whose pioneer works on Missouri herpetology have been often quoted.

In 1893 (p. 258) Hurter wrote that he had taken only 2 *Lygosoma* up to that time. These same specimens were mentioned again in 1897 (pp. 502-503) when he stated that, "This nimble animal is quite common in all the Southern States, and also in all the southern counties of Missouri, but it reaches its most northern recorded limit at Cliff Cave, only eleven miles south of the city of St. Louis, where we have collected so far two specimens. As soon as we come to Jefferson County, they become more plentiful." Little was added to this account in 1911 (p. 144) except for the mention of an additional specimen from St. Louis County.

Today, *Lygosoma* is also common in parts of Lincoln and Montgomery counties, including the vicinity of Montgomery City, from where Hurter was sent herpetological specimens by one Edgar M. Parker, and where he collected personally on occasion. Yet he stated (1911: 144) that he was unaware of the species being found north of the Missouri River.

Although data suitable for statistical analysis are not available, a population growth and possibly a range extension of *Lygosoma* do appear to have occurred, at least in east-central Missouri. The ecology of the Ground Skink is poorly known, barring the presentation of a hypothesis at this time.

REFERENCES

Hurter, Julius. 1893. Catalogue of reptiles and batrachians found in the vicinity of St. Louis, Mo. Trans. Acad. Sci. St. Louis 6(11): 251-261.

———. 1897. A contribution to the herpetology of Missouri. *Ibid.* 7(19): 499-503.

———. 1911. Herpetology of Missouri. *Ibid.* 20(5): 59-274, pls. 18-24.

Myers, C. W. 1957. Amphibians and reptiles of Washington State Park, Washington County, Missouri. Trans. Kansas Acad. Sci. 60: 288-293.

Odum, E. P. 1953. Fundamentals of ecology. Philadelphia, W. B. Saunders.

CHARLES W. MYERS

DEPARTMENT OF BIOLOGY
UNIVERSITY OF FLORIDA
GAINESVILLE

A DEVICE FOR SEPARATING SALMON FRY OF UNEQUAL SIZE

INTRODUCTION

With the sharp decline of southeastern Alaska pink salmon (*Oncorhynchus gorbuscha*) runs, the U. S. Fish and Wildlife Service broadened its research program in 1951 to include an intensive study of the ocean life of this species. A part of this program included the marking, by fin-clipping, of several thousands of pink salmon fry annually. Their return, some 14 months later as marked adults, provided a means of assessing ocean mortality.

The authors are indebted to Virginia Coleman, illustrator for the Fish and Wildlife Service at Seattle, for Figure 1.

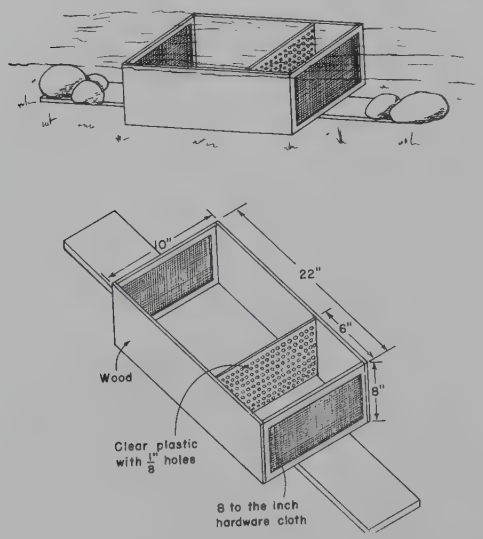

FIG. 1. Fry-separating device of the type used.

METHODS

A problem confronting the investigators during trapping of the pink salmon fry was the concurrent heavy migration of chum salmon fry (*O. keta*). Since the fry of this species were only slightly larger than those of the pink salmon, marking speed was materially reduced when the 2 remained mixed through the fin-clipping process.

It was reasoned that the natural disparity in size between the two species might allow the fry to separate themselves. Theoretically, mixed fry could be introduced within a device containing openings through which only the pink salmon could escape. After a period of trial and error, a wooden box 10 inches wide, 8 inches deep, and 22 inches long was constructed (Figure 1). The top and both ends were open, with the latter covered by 8-mesh hardware cloth. In use, the device was placed in shallow water, allowing the current to flow through its long axis and causing the fish to orient themselves toward the upper end. Rocks, piled on a "foot" protruding from the bottom at either end, held the box securely in position. A clear plastic partition 3/16-inch thick, through which 200-300 holes 1/8 inch in diameter had been drilled, was inserted 6 inches from the downstream end. Approximately 1,500 mixed fry were then introduced into the downstream or smaller compartment.

RESULTS

Over 100 pink salmon fry per minute escaped through the partition into the upstream or larger compartment, where they needed only to be removed for marking. Only the very small chum salmon fry escaped. By actual count, the separating device proved nearly 90 per cent efficient in removing the pink salmon fry. It was noted that the more crowded the mixed fry were, the greater the escapement rate.

ALTON Y. ROPPEL
AND
CHARLES R. WEAVER

U. S. FISH AND WILDLIFE SERVICE
SEATTLE, WASHINGTON

THE EFFECT OF TEMPERATURE ON GROWTH AND REPRODUCTION IN *CRASPEDACUSTA SOWERBII*[1]

Information concerning the effect of temperature on the life cycle of marine hydrozoans appears to be limited, although there are studies on the effect of temperature change on seasonal settlement patterns of marine invertebrates including hydroids (Fuller 1946, Graham 1945, Weiss 1948); and seasonal variations in the growth of *Obelia* have been recorded (Hammett 1945). The literature is more extensive for fresh-water hydrozoans, and hydras have been studied both under natural conditions and in the laboratory (Hyman 1928, Loomis 1954, McGill 1908, Miller 1936, Welch 1924).

[1] The author wishes to thank Dr. Frederick E. Smith for his advice in the preparation of this paper.

The fresh-water Coelenterate *Craspedacusta sowerbii*

has a life cycle similar to that found in marine members of the class Hydrozoa and, as the hydroid stage of *Craspedacusta* may be easily cultured in the laboratory, a study was made of the effect of temperature on the reproductive activity of this animal. It is hoped that the results obtained may also be of value in understanding the life cycle of marine hydrozoans.

The hydroid stage of *Craspedacusta* consists of a colony of one to 10 polyps attached to rocks, aquatic vegetation, or other material in a variety of fresh-water habitats. An average polyp is about one millimeter long, lacks tentacles, and resembles a bowling pin in shape. The food of *Craspedacusta* consists of a variety of small invertebrate forms. In younger colonies polyps have a common coelenteron; later this connection appears to become reduced or obliterated.

The hydroid stage undergoes 3 types of reproduction. The first of these is a budding of new polyps which remain attached to the parent polyp. The second is by frustules, cylindrical bodies which leave the parent polyp, subsequently developing into new colonies. The third is by means of medusa buds, which detach from the parent polyp as free swimming medusae. Frustule and polyp buds appear in all seasons except winter. Medusa buds are formed only in summer and early fall.

The following papers may be consulted for various aspects of the life history and ecology of *Craspedacusta;* Dejdar 1934; Dexter 1949; Kuhl 1947; Payne 1924, 1926; Pennak 1956. Those of Dedjar and Payne are especially valuable as regards hydroid morphology, budding and development.

Method

Colonies growing on rocks were collected October 7 and 10, 1957 from a creek which empties into the Huron River seven miles northwest of Ann Arbor, Michigan. *Craspedacusta* was first collected from this creek in 1941 (Woodhead 1943). Water temperature at the time of collection was 11°C. No medusa buds were observed on the material collected, although frustule buds and frustules were present. The collected colonies were kept in complete darkness at 20°C, and were fed brine shrimp of the kind commonly used to feed aquarium fish. Feeding resulted in the production of enough frustules to enable controlled cultures to be set up on October 20th. Cultures were set up at 33°C, 28°C, 25°C, and 12°C. Three finger bowls were set up at each temperature, each bowl being seeded with 15 frustules. One bowl was seeded with frustules averaging .4 millimeters in length, a second with frustules averaging .5 millimeters, and a third with frustules averaging .6 millimeters. An additional 3 finger bowls were set up at 20°C on November 4th. Material for these cultures was collected on October 20th, under conditions similar to the initial collection.

Water in the finger bowls was changed once a week with filtered water from the original collection site. All bowls were kept covered and in complete darkness. At intervals of 3 days, each polyp was fed a brine shrimp. The brine shrimp used were hatched in .4% salt solution, and rinsed in 3 changes of tap water. Early in the experiment small polyps did not take shrimp. After the first week, however, all polyps ate regularly. Observations of budding behavior were made every other day for a period of 102 days. Since there was no significant difference between them, the 3 finger bowls at each temperature were treated as a unit in making tables and graphs. On December 11th the 2 finger bowls at each temperature originally seeded with the smaller frustules were discontinued, leaving one finger bowl per temperature for the remainder of the experiment.

Results

Colony Growth

Two to 10 days after seeding, frustules differentiated into polyps at one or both ends, and were then considered to be colonies. At 28°C, 97% of the frustules developed polyps at both ends, 70% did so at 25°C, 85% at 20°C, and 3% at 12°C. Subsequent colony growth as measured in terms of polyps per colony is shown in Figure 1. Although initially the cultures maintained at 12°C had the fewest number of polyps per colony, by the end of the experiment they had the largest number (5 per colony). Three weeks after the end of the experiment there were 5.9 polyps per colony at 12°C, 3.8 at 28°C. At 33°C colony growth was very irregular, many newly formed colonies shortly regressing, and then subsequently reforming, only to regress again. From the 45 frustules seeded at this temperature, only 10 colonies were formed, and these were generally reduced in size, indicating that 33°C was above the optimum range for *Craspedacusta.* The data for this temperature were not considered sufficient to graph.

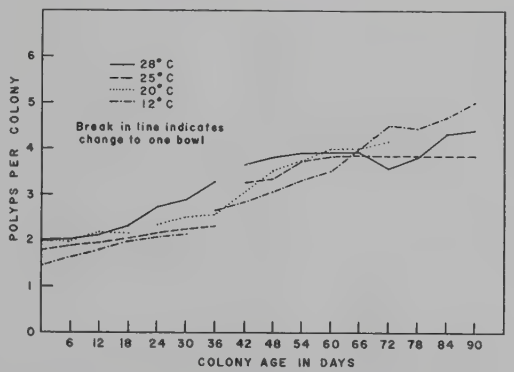

Fig. 1. Growth of hydroid colonies at different temperatures. Growth measured in terms of number of polyps per colony. In order to allow sufficient time for all frustules to differentiate into polyps, colony age 0 was 12 days after initial seeding with frustules.

Budding

As the polyp was the feeding unit, rather than the colony, it seemed best to relate budding activity to the number of polyps present rather than to the number of colonies present.

Observation indicated that a period of time usually passed before newly formed polyps first began to bud. Since it was desirable to relate reproductive activity only to polyps that were mature (capable of budding), the following procedure was used to obtain at least a crude measure of the time at which a polyp could be considered mature: At 28°C medusa buds developed slowly enough so that a polyp's age at the time it first produced a medusa bud was always known. At this temperature it was therefore possible to graph the percentage of polyps that had budded at least one medusa against the polyps' age (Figure 2). Using this graph, all original polyps (those developed from seeded frustules) were considered capable of medusa budding when 24 days old, secondarily formed polyps (those budded from original polyps) when 4 days old. As can be noted from the graph, once budding be-

gan it followed a similar curve in the case of both original and secondary polyps. The major difference was the greater time period needed for original polyps to mature. Frustules budded off too rapidly to be traced to their parent polyps, so it was not possible to tell when a polyp first became capable of frustule budding. However, as frustules began to appear in the 28°C cultures 6 days before medusae, polyps at this temperature were considered capable of producing frustules at 18 days (original polyps) and 1 day (secondary polyps). Since the 20°C and 25°C cultures were the same age as the 28°C cultures when frustules first appeared, maturity ages of 18 days and 1 day were also used for these two temperatures. In the 12°C cultures frustules began to appear 12 days later that at the 3 other temperatures, so the maturity dates were therefore set as 30 days and 10 days.

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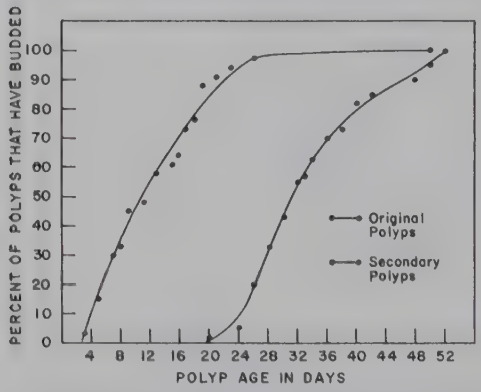

FIG. 2. Relation at 28°C between polyp age and ability to produce medusa buds. Original polyps as a group were considered mature (capable of medusa budding) at an age of 24 days; secondary polyps at 4 days. Curves drawn by inspection.

Since the parents of polyp buds were known, the procedure used in determining medusa budding capability was also used for polyp budding. No clear effect of temperature was evident, and polyps at all temperatures were considered capable of polyp budding when 20 days old.

Figure 3 shows the average numbers of the three kinds of buds produced per mature polyp during 102 days. Since the 20°C cultures ran for only 84 days, an estimate was made of their budding performance for the remaining 18 days. There is a striking difference in the relative numbers of bud types, frustules far outnumbering the others at all temperatures. Both frustule and polyp bud production appeared to change gradually with temperature. Frustule budding reached a maximum at 25°C at which temperature polyp budding was minimal.

Medusa buds were produced in the 28°C culture, and to a limited extent, in the 33°C culture. At 28°C, 74% of all buds were frustules, 22% were medusae, and 4% were polyps. Medusa budding, unlike the other types of

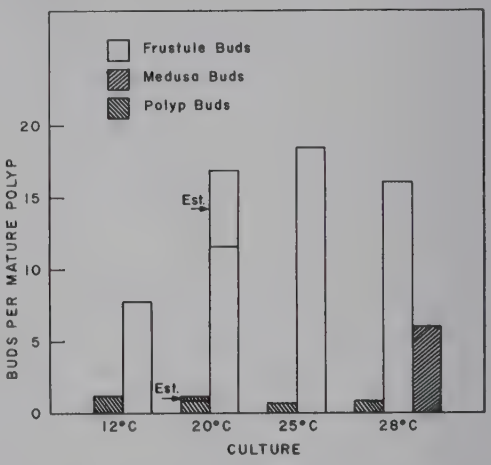

FIG. 3. Number of buds per mature polyp over 102 day period. Data for medusa and frustule budding were determined by counting medusae and frustules one to two days after release from their parent polyps. Polyp buds were recorded when first observed. The 20°C cultures were run for only 84 days and bud production for the last 18 days was an estimate.

budding, occurred within a fairly narrow temperature range. At 28°C an average polyp produced a medusa bud every 17 days. In contrast, at 33°C, 15 polyps produced 21 medusa buds over a 37 day period, or an average rate of one bud per polyp every 26 days. Therefore it is probable that 33°C was near the upper temperature limit at which medusa budding could occur.

At the end of 102 days, the culture which had been maintained at 25°C and had produced no medusae, was changed to 27°C, and several medusa buds appeared on culture polyps, indicating a minimum medusa producing temperature of about 26°C under the described laboratory conditions.

Medusa budding at 28°C began when the cultures were 18 days old and showed a fairly steady rise, leveling off after 8 weeks at which time .55 medusae were produced per mature polyp every 6 days.

Two patterns appeared in frustule production (Figure 4). At 28°C frustule production apparently reached a peak in 54 days with a subsequent decline. Frustule production at all other temperatures showed a slow increase which continued to the end of the experiment.

No apparent trend could be seen in polyp bud production. Budding was sporadic, showing no definite increase or decrease. At 28°C an average mature polyp produced .9 polyp buds over the 102 day period of the experiment. Figures for the 25°C, 20°C and 12°C cultures were .7, 1.17 and 1.23 polyp buds per mature polyp.

From the above data it would therefore appear that polyps were able to maintain their reproductive activity over a period of at least three months.

Bud Size and Location

In the 28°C cultures the diameter of newly formed medusae, as measured one to two days after release, ranged between .5 and 1.3 millimeters throughout the 102 day period.

Comparative measurements of the size of frustules at

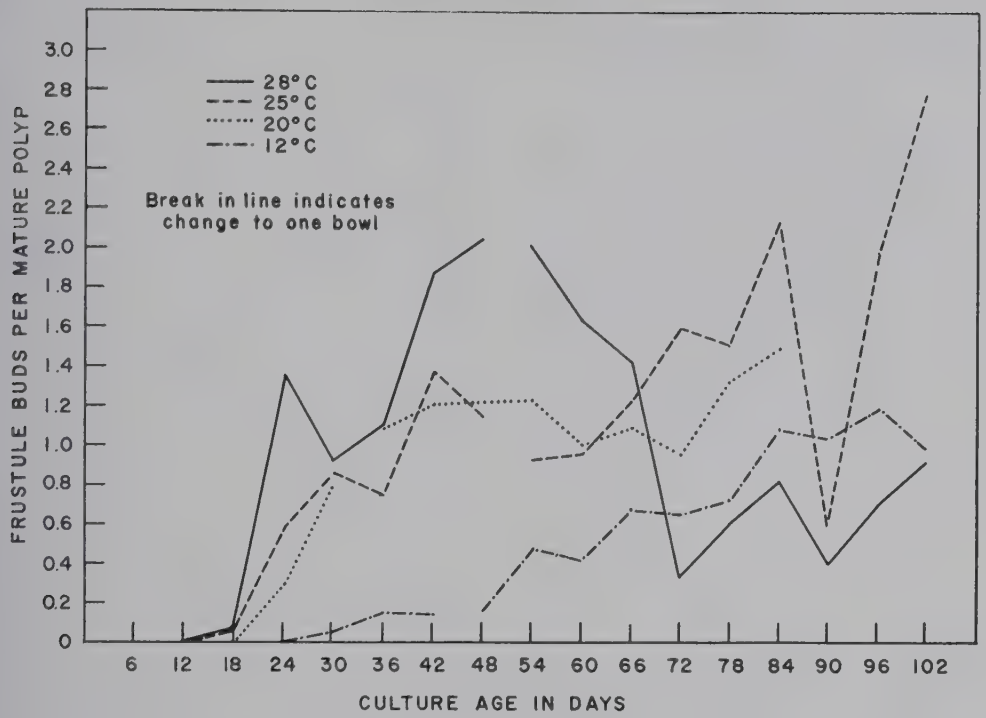

FIG. 4. Rate of frustule production. Figures in terms of frustule buds per mature polyp at six day intervals.

different temperatures were made. The frustules were divided into three groups based on length. Group one consisted of frustules under .4 millimeters in length; group two, frustules between .4 millimeters and .6 millimeters in length; and group three, those over .6 millimeters in length. In the 28°C cultures 1177 frustules were measured; in the 25°C cultures 973; in the 20°C cultures 594; and in the 12°C cultures 290. At 28°C, 76% of the frustules were in group one, 23% in group two, and 1% in group three. Respective percentages for 25°C were 24%, 56% and 20%; for 20°C, 29%, 52%, and 19%; and for 12°C, 46%, 42% and 12%.

Although no measurements were recorded, frustules in the 25°C cultures were commonly thicker and more opaque than those in the 28°C cultures. Frustules in the 20°C and 12°C cultures were intermediate in this respect.

Polyp buds were measured on first appearance and again after 10 days. The percentage increase in bud length over this time interval was then graphed (Figure 5). Optimum temperature for polyp bud growth was 25°C.

Frustule and medusa buds most commonly were formed in the middle portion of a polyp. Out of a total of 282 frustule buds observed while still attached to the parent polyp, 257 (91%) were located on the middle third of the parent polyp. Seven (3%) were located on the distal third and 18 (6%) on the proximal third. Of 248 medusa buds observed in the 28°C cultures, 209 (84%) were located on the middle third of the parent polyp; 3 (1%) were located on the distal third, and 36 (15%) on the proximal third. No data were taken on polyp bud location.

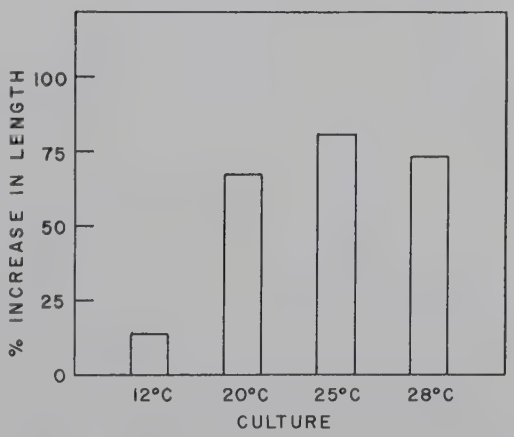

FIG. 5. Relative polyp bud growth over a ten day period. Bud length was measured at first appearance of bud and again after 10 days. (Data on basis of 28 buds at 12°C, 9 at 20°C, 25 at 25°C, 40 at 28°C.)

CONCLUSIONS

Over the 102 day period of the experiment 25°C appeared to be the optimum temperature for growth and reproduction in *Craspedacusta*. At this temperature frustule production, frustule size and polyp bud growth were all maximal. At 12°C frustule budding capacity decreased, but colony growth at the end of 102 days, as measured in terms of polyps per colony, was greatest.

At temperatures above 25°C frustule production appeared to drop off from its optimum and reproduction by medusa buds appeared.

Summary

1. The effect of 5 temperatures, 33°C, 28°C, 25°C, 20°C, and 12°C, on hydroid budding in *Craspedacusta sowerbii* was studied over a 102 day period.

2. Frustule buds were the most common form of buds at all temperatures, polyp buds the least. Medusa buds were formed only within a narrow temperature range, falling approximately between 26°C and 33°C.

3. As measured in terms of buds per mature polyp the optimum temperature for frustule budding was 25°C; for polyp budding, 12°C and 20°C.

4. Frustule budding reached a peak in 54 days at 28°C, and subsequently declined. At 102 days frustule budding at other temperatures was still increasing. No trend was apparent in medusa or polyp budding.

5. Frustule size and polyp bud growth were found to be greatest at 25°C.

6. Frustule and medusa buds typically were formed in the middle of a polyp.

References

Dejdar, E. 1934. Die Süsswassermeduse *Craspedacusta sowerbii* Lankester in monographischer Darstellung. Zeitschr. Morph. Ökol. Tiere **28**: 595-691.

Dexter, R. W., T. C. Surrarrer, and C. W. Davis. 1949. Some recent records of the fresh-water jellyfish *Craspedacusta sowerbii* from Ohio and Pennsylvania. Ohio Jour. Sci. **49**: 235-241.

Fuller, J. L. 1946. Season of attachment and growth of sedentary marine organisms at Lamoine, Maine. Ecology **27**: 150-158.

Graham, H. W., and H. Gay. 1945. Season of attachment and growth of sedentary marine organisms at Oakland, California. Ecology **26**: 375-386.

Hammett, F. S., and D. W. Hammett. 1945. Seasonal changes in *Obelia* colony composition. Growth **9**: 55-144.

Hyman, L. H. 1928. Miscellaneous observations on Hydra with special reference to reproduction. Biol. Bull. **54**: 65-108.

Kuhl, G. 1947. Zeitrafferfilm-Untersuchungen über den Polypen von *Craspedacusta sowerbii*. Abhandl. Senckenberg. Naturforsch. Ges. **473**: 1-72.

Loomis, W. F. 1954. Environmental factors controlling growth in Hydra. J. Exp. Zool. **126**: 223-234.

McGill, C. 1908. The effect of low temperatures on Hydra. Biol. Bull. **14**: 78-88.

Miller, D. E. 1936. A limnological study of *Pelmatohydra* with special reference to their quantitative seasonal distribution. Trans. Amer. Micros. Soc. **55**: 123-193.

Payne, F. 1924. A study of the fresh-water medusa, *Craspedacusta ryderi*. J. Morph. **38**: 387-430.

———. 1926. Further studies on the life history of *Craspedacusta ryderi*, a fresh water hydromedusan. Biol. Bull. **50**: 433-443.

Pennak, R. W. 1956. The fresh-water jellyfish *Craspedacusta* in Colorado with some remarks on its ecology and morphological degeneration. Trans. Amer. Micros. Soc. **75**: 324-331.

Weiss, C. M. 1948. The seasonal occurrence of sedentary marine organisms in Biscayne Bay, Florida. Ecology **29**: 153-172.

Welch, P. S., and H. A. Loomis. 1924. A limnological study of *Hydra oligactis* in Douglas Lake, Michigan. Trans. Amer. Micros. Soc. **43**: 203-235.

Woodhead, A. E. 1943. Around the calendar with *Craspedacusta sowerbii*. Trans. Amer. Micros. Soc. **62**: 379-381.

Andrew McClary

Department of Zoology
University of Michigan
Ann Arbor, Michigan

THE USE OF RADIOACTIVE PHOSPHORUS IN THE STUDY OF COLONY DISTRIBUTION OF THE ANT *LASIUS MINUTUS*

Introduction

Studies of the ecological distribution of ants are concerned with the occurrence of colonies of ants, not of individual workers, because the colony is the unit of social organization. Hence, recognition of what constitutes a colony is essential to the accurate completion of such studies. Usually the inhabitants of a single nest structure are thought to comprise a colony. But it is difficult to be certain that each nest structure is really independent and that there is not a direct overground or underground connection with neighboring nest structures. This very problem was attacked by Headley (1941) in a study of the crater nests of *Lasius neoniger* Emery (= *Lasius niger alienus americanus* Emery). Although his data suggested that a colony may have several craters, he was unable to demonstrate this conclusively.

Some species of ants may be sufficiently constant in their nest site and structure to make recognition of the limits of the colony simple (*e.g., Dolichoderus mariae* Forel, which has solitary domes—at least in southeastern Michigan). However, other species occupy sites in which the colony may be spread over a considerable area and/or may be in several structures which are not necessarily contiguous (*e.g., Leptothorax curvispinosus* Roger, the colonies of which are found in hollow acorns and stems lying on the ground). The mound-forming species are especially important because their nests are large and conspicuous and because they are frequently used in ecological studies. Colonies of some species evidently have monodomous nests, *i.e.,* they occupy only a single mound each. Colonies of other species apparently live in two or more interconnected mounds each and have, therefore, polydomous nests.

I have recently completed a study of bog-inhabiting ants in southeastern Michigan. During the course of this investigation the mounds occupied by *Lasius minutus* Emery in a ten acre section of swamp and marsh on the Edwin S. George Reserve, Livingston County, Michigan, were counted, and the location of each mound was plotted on a large scale map of this area (Figure 1). This work was done in March and April of 1956, a time when neither vegetation nor snow obscured the mounds. The distribution of the mounds appeared to me to be clumped. If this were true, then each cluster of mounds probably

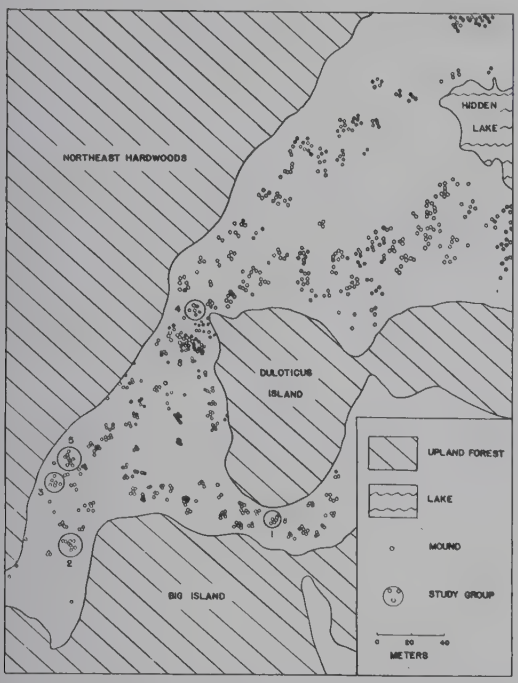

FIG. 1. Diagram of the occurrence of *Lasius minutus* mounds in a ten acre portion of the Big Swamp on the Edwin S. George Reserve, Livingston County, Mchigan, in the spring of 1956. Drawing prepared by Miss Patricia Borgman from aerial photographs provided by I. J. Cantrall.

arose by colony division from a single original mound. Mounds that remained interconnected would all be part of a single colony. Lack of connection between mounds would indicate that each mound housed a separate colony now independent from the parent colony.

The workers of a *Lasius minutus* colony are hypogeic, appearing rarely on the surface. I have found workers on the nest surfaces only during the nuptial flights, which take place on afternoons in late August and early September (Kannowski 1958), and during several brief periods of the year when it is necessary to rebuild or enlarge the nest. Most of this latter work takes place from evening to early morning. No movement was observed between mounds at these times. A major function of the colony is the maintenance of aphids (mostly *Prociphilus* sp., determined by Louise M. Russell) which they guard and from which they obtain most, if not all, of their food (in the form of honeydew). The aphids occur exclusively on roots and underground stems, apparently always of grasses and sedges. In their cultivation of these aphids the *L. minutus* workers build tunnels leading away from the mound just beneath the surface of the soil. These tunnels may connect adjacent mounds, but are virtually impossible to trace by excavation because of the soft, mucky soil. All attempts to follow the tunnels in this manner failed.

The use of radioisotopes in the study of territorialism in ants was first suggested by Pendleton and Grundmann (1954). They injected radioactive phosphorus (P^{32}) into the tissues of a thistle plant and traced the isotope through the plant to aphids feeding on the stems. The phosphorus appeared in the honeydew which was secreted by the aphids and which was collected by certain ants. These ants were then traced to their nests. Such a technique would not be very practical in the case of ants tending root aphids, for there are many problems in locating the aphids on the proper roots. However, ants that feed upon honeydew will probably eat honey. By placing honey mixed with P^{32} in a single mound, some workers of that mound might feed upon it and pass it on to others in the colony. Periodic sampling of the neighboring mounds for radioactive ants might indicate whether or not the mounds are interconnected. Such a procedure was first planned in the spring of 1955, but could not be carried out until the summer of 1957.

ACKNOWLEDGMENTS

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METHODS

Five groups of mounds of *L. minutus* were selected for study in a part of the Big Swamp on the George Reserve in 1957 (Figure 1). The Big Swamp is a lowland of about 200 acres occupied mainly by a larch-poison sumac community. Frequently separating this community from the surrounding uplands are fern-sedge-grass marshes. It is in these marshes and the ecotones between the marshes and the larch-poison sumac community that the mounds of *L. minutus* are most numerous.

Each mound was staked, and the natural radioactivity of the ants in them was checked. A more or less centrally located mound in each group was marked to receive a source of radioactive material (hereinafter referred to as the "source" mound). Radioactive phosphorus was mixed with commercial honey, which was then placed in the "source" mounds. One mound received 4 ounces of honey containing approximately 7.9 millicuries of P^{32}. One ounce of honey containing about 2 millicuries of P^{32} was placed in each of the other four "source" mounds. Beginning about 6 to 8 hours after the food was introduced, samples of 15 workers each were collected twice a day from the mounds in each group. Whenever possible, larvae and pupae were also collected. However, in order to hold disturbance of the mounds to a minimum, the nests were opened only superficially, and consequently, it was not always possible to obtain a sample of the brood. The ants were killed in alcohol and dried under a heat lamp. Each sample was then placed in a scaler-counter, and the radioactivity recorded in distintegrations per minute. Samples that were "cold" (radiation not significantly greater than background) were discarded. The "hot" samples were analyzed to find the proportion of workers and brood that were radioactive and to determine the variation in radioactivity of the individual ants. All mounds were checked for about one week after the introduction of the radioactive honey. Thereafter, those mounds which still showed no evidence of radioactivity ("non-radioactive" mounds) were checked intermittently for one to 3 weeks. A portable Geiger-Muller counter was used in the study area to locate "radioactive" mounds, but always a sample of ants was collected to be checked

in the scaler-counter. I soon discovered that the radioactivity of ants in some mounds was too slight to be adequately indicated by the Geiger counter.

Results

One of the 5 "source" mounds proved to be solitary (group #1), as no evidence of radioactivity was found in any other mound in this group. The other 4 groups each comprised 4 or more interconnected mounds (Figure 2),

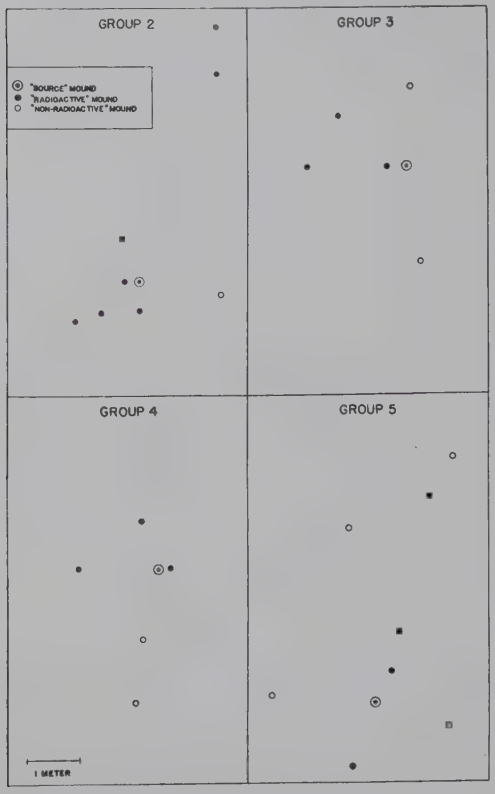

Fig. 2. Location of *Lasius minutus* mounds in four study groups. After feeding honey mixed with radioactive phosphorus to the "source" mounds, radioactive ants were found in each "radioactive" mound. In each group all mounds containing radioactive ants were components of a single colony.

the largest group consisting of 8 mounds. Twenty-two mounds in the 5 groups contained radioactive ants, giving a mean of 4.4 mounds per colony. It developed that several of the "source" mounds were off center with reference to the rest of the mounds in the cluster (groups #3 and 5). This is particularly evident in group #5 where the mounds have a linear arrangement.

Most mounds within 1½ meters of a "source" mound were interconnected with it. Beyond this distance mounds that were independent or part of another cluster were frequently encountered. The greatest distance separating 2 mounds of the same colony was aproximately 6.5 meters in group #2. The number of mounds in a cluster and the distances separating them are probably indications of the age of the colony. New colonies are undoubtedly monodomous, becoming polydomous as the colony gets older. As the number of mounds increases, the distance between the terminal mounds probably also increases, although this probably depends upon the growth pattern of the colony. After many years the colony may begin to die out with the mounds being gradually abandoned.

If a colony is originally monodomous, it may become polydomous in one of two ways: 1) by the union of two existing colonies; and 2) by forming new mounds connected to the original. Neither of these conditions has been observed. However, I believe that the second hypothesis is valid for most, if not all, cases. The tunnels in the soil are evidently the only connections between mounds. In some places gumdrop-shaped mounds, 8 to 25 centimeters high, are formed in which several clusters of aphids are found. These "micromounds" are evidently incipient mounds, each of which may be a nucleus for later expansion. If this is true, then the secondary mounds of the colony start out as enlarged feeding areas and are later converted to regular mounds with brood chambers.

The direction of growth of a colony, thus, is probably determined by the arrangement of the tunnels. If tunnels radiate in several directions from the original mound, there may be a close cluster; if there is a single tunnel or 2 tunnels in the same axis, a linear arrangement may prevail.

When the ants were first checked they had already carried the food to all of the inter-connected mounds in groups #3, 4, and 5. It is possible that this is also true for group #2, but the 2 most distant mounds in this group were overlooked, and thus not checked in the first 2 days. The fact that this food has spread throughout the 3 colonies in the first 6 to 8 hours is remarkable because the food was placed in the mounds at a time when the natural food supply was probably abundant. Hence, an immediate transmission to most of the colony members was not expected.

Six to 8 hours after the honey was placed in a "source" mound, more than 50% of the larvae that were sampled in that mound were found to be radioactive, but at the same time less than 50% of the larvae from the adjacent "radioactive" mounds were radioactive. In addition, the larvae in "source" mounds had several times the radioactivity of those of the "radioactive" mounds. In the latter mounds the percentage of radioactive larvae and the intensity of radiation of the larvae were highest in groups #3 and 4 which had the fewest mounds. The larvae, as a group and individually, showed much less radioactivity than the workers of the same mound, undoubtedly because they received a smaller quantity of food. Those ants (both workers and larvae) nearest the source of the food probably had first chance at the food and got most of it.

Wilson and Eisner (1957) in a series of laboratory experiments fed a mixture of honey and radioactive iodine (NaI^{131}) to a single worker in each of several colonies of 5 species of ants (none *Lasius*) and traced the honey throughout each colony. They discovered that the larvae and queens were among the last to receive the food. The present experiments with natural colonies of *L. minutus* indicate that the workers feed first on the food and pass it on to other workers and then feed the larvae. This probably happens because the workers are more easily able to obtain food from the food carriers than are the larvae. Wilson and Eisner explained the slow transmission of food to the larvae as probably the result of

differential feeding. Thus, in their laboratory colonies the larvae received little of the liquid honey because they do not normally feed on this type of food. While this may be true for some species, I doubt whether differential feeding occurs in *L. minutus* colonies, because of the almost complete dependence of all members of the colony on a single food.

The difference in the speed of transmission to the larvae observed by Wilson and Eisner and that which I found seems mainly due to the amount of food given the colonies, but perhaps also to the feeding habits of the several species. Wilson and Eisner allowed their colonies only a minute amount of food to be passed throughout the colony, while I gave my mounds relatively huge quantities of food. So far as I know, none of the 5 species studied by Wilson and Eisner feed exclusively on a natural food similar to honey. Most of them probably feed to a small extent on such foods. On the other hand, *L. minutus* must live almost exclusively on this type of food. Because *L. minutus* colonies apparently always tend large numbers of root aphids, there is probably a large supply of food continuously available to the colony (during the growing season) and this probably is transmitted to both larvae and workers rather quickly.

Seven days after one mound received the honey, radioactive pupae (all immature) were found. Careful analysis showed that most of the radioactivity resided in the tissues of the pupae and very little in the pupal cases. Thus, these pupae must have received radioactive food when they were larvae. More mature pupae tested at the same time showed radioactivity close to the background radiation, indicating that they had pupated before the colony was fed. This also showed that very little radioactivity was picked up on the pupal cases from the soil of the nest and from the activities of the workers in moving the pupae about.

Summary

Five widely separated groups of mounds of the ant, *Lasius minutus* Emery, were studied in a swamp in southeastern Michigan to determine whether or not each mound represented a separate colony. Honey mixed with radioactive phosphorus was placed in one ("source") mound in each group. The ants fed upon the honey and passed it on to others in the colony. Ants in certain adjacent mounds were found to be radioactive in 4 of the 5 groups indicating that the "source" mounds were interconnected with other mounds. Hence, a colony of *L. minutus* actually consists of one or more mounds. Transmission to the other mounds of the colony was found to occur within the first 6 to 8 hours. Within this time both workers and larvae had received the food. The intensity of radiation of the ants and the percentage of radioactive ants in a mound were greatest in the "source" mounds and in the "radioactive" mounds nearest to them.

References

Headley, A. E. 1941. A study of nest and nesting habits of the ant *Lasius niger* subsp. *alienus* var. *americanus* Emery. Ann. Ent. Soc. Amer., **34**: 649-657.

Kannowski, P. B. 1958. The flight activities and colony-founding behavior of bog ants in southeastern Michigan. Insectes Sociaux. In press.

Pendleton, R. C. and A. W. Grundmann. 1954. Use of P^{32} in tracing some insect-plant relationships of the thistle, *Cirsium undulatum*. Ecology, **35**: 187-191.

Wilson, E. O. and T. Eisner. 1957. Quantitative studies of liquid food transmission in ants. Insectes Sociaux, **4**: 157-166.

Paul B. Kannowski

Department of Biology
University of North Dakota
Grand Forks, North Dakota

AREAS OF DISCOVERY IN THE EPHESTIA-IDECHTHIS ECOSYSTEM DELIMITED BY VERMICULITE

In order that the *Ephestia-Idechthis* ecosystem (described in Ecology 39(3): 545-547) may be used efficiently in the study of populations as affected by areas of discovery differing in size relative to constant amounts of a host supporting medium, it is essential that these areas of discovery consist of inert, non-edible material which will be subject to invasion by the susceptible stages of the host. Tests have shown that a light-weight mineral such as expanded mica (vermiculite) can be used for this purpose.

The minimum amount of vermiculite used in each ecosystem is determined by the reach of *Idechthis* (6 mm) and the surface area of the host-edible material to be covered.

It has been demonstrated that when the area of discovery is delimited by vermiculite it may be invaded by at least 50% of the host population as indicated by the population parasitized.

With areas of discovery delimited by vermiculite the use of very small amounts of host-edible material will not necessarily result in the complete elimination of the host by the parasite. Such elimination will occur when all of the host-edible material is incorporated in the area of discovery.

S. E. Flanders

Citrus Experiment Station
University of California
Riverside, California

REVIEWS

A Descriptive Population Ecology of Land Animals[1]

Tischler's moderate-sized volume features well-organized accounts of the distribution, numbers, and biomass of land animals in various habitats. The literature of northern Europe is well covered, and there are frequent samples from North America, Russia and the tropics. The emphasis is on ecological structure (that is, the pattern of the "standing crop") at the population level. Plants and microorganisms are largely considered as a part of the animal's environment rather than as integral parts of the community. However, considerable emphasis is placed on interrelations of animal populations and on qualitative food webs. There is a short chapter entitled "Energie und Stoff im Ökosystem," but this is concerned mostly with "Stoff" and very little with energy.

A very attractive feature of the book is the large amount of illustrative material comprising charts, graphs, pictorial diagrams and tables (a total of 116 figures and 21 tables). Many of these illustrate seasonal and successional changes in populations as well as zonations of various sorts; as such, they are very instructive and contribute to the discussion in the text. On the other hand about 20 of the figures (16% of the total) are what one might call "arrow diagrams" which attempt to elucidate food webs; to the present reviewer these complex diagrams are quite frustrating in that they detract rather than add to one's understanding of natural populations. While "arrow diagrams" are often useful for illustrating biogeochemical cycles and the very broad aspects of food chains, they become completely unintelligible and misleading when applied to the details of community dynamics. For one thing such diagrams are not quantitative; the arrows are all of the same magnitude giving the entirely false impression that all the illustrated pathways are of equal importance and that all are functioning at the same time. Also, the diagrams give a misleading impression regarding the number of steps in food chains because no distinction is made between the cycling of materials and the one-way flow of energy. In other words the kind of information shown in Tischler's complex diagrams would be much better presented in tabular form, or in bar graphs where the quantity (or at least percentage) of food items could be shown more accurately. It is to be hoped that the energy flow diagram will replace the elaborate food web diagram in future ecological literature!

The book is divided into two parts, one entitled "General Synecology," the other "Special Synecology." In the first part environmental conditions (especially climate and soil) influencing animal populations are considered along with spatial arrangements, zonation and succession of the populations themselves. Also discussed in some detail in the first section are interspecific relationships such as competition (emphasizing Gausian concepts), parasitism, mutualism, periodicity, and influence of man on nature. In the second part of the book the animal populations of major "landscape types" (or "biomes" as American ecologists might call them), as, for example, tundra, taiga, deciduous forest, etc., are considered. Included under a separate subdivision are very interesting descriptions of populations of agricultural lands ("Kulturlandschaft") such as fields and gardens. Comparison of these man-stabilized communities with less disturbed communities raises many fundamental questions which are of vital importance to man as he brings more and more land under close control. It is evident that most of these questions cannot be answered by descriptive study alone; functional and experimental work is also needed.

For the American reader the review of the very extensive literature on soil fauna of Northern Europe is an especially valuable feature of the book. There is no comparable literature in North America. In a recent visit to several centers of ecological research in northern Europe the reviewer was impressed with the large amount of background knowledge in basic soil ecology which has been accumulated. Leading workers in this field are now turning from the work of counting and enumerating species, which formerly occupied most of their energy, to studies of actual roles of the organisms in the metabolism of the soil. For the latter, they probably have a head start over workers in the United States, where the soil biota is very poorly known. However, since soils of Europe and of at least northern U. S. should be similar the ecologist in this country would do well to consult the European literature. Tischler's book is a good place to begin.

One of the difficulties in developing a satisfactory synecology of animals is the fact that animals associated together in a given area of the earth's surface vary widely in size and rate of metabolism. Consequently, numbers tend to overemphasize and biomass underemphasize importance of small organisms in the community, while the reverse tends to be true with large organisms. Therefore, only by integrating changes in numbers and biomass and determining population energy flow can diverse populations be compared in so far as their true role in the ecosystem is concerned.

In summary, few new ecological principles are introduced in this book. This is not a criticism because it is evident that Professor Tischler's objective was a comprehensive review of the composition of animal components of land ecosystems. If graduate students or other investigators are looking for good problems, this book will suggest many, and it will provide excellent background information necessary for the solution of specific problems.

Eugene P. Odum

Department of Zoology
University of Georgia

[1] Tischler, Wolfgang. 1955. Synökologie der Landtiere. Stuttgart: Gustav Fischer Verlag. xiv + 414 pp., 116 figs. DM 36.—, $9.00.

A Marine Ecology Book with the Factor, Life History, and Habitat Approach[1]

In eighty years of journals and expedition volumes lie lovely little stories on the life of marine creatures and hypothetically pertinent distributions of environmental properties. Much of the fascination of the sea is in the delightful mysteries of odd organisms and situations, whether portrayed in the color photography of the popular literature or in the diagrams and graphs of the biologist. In a new book with detailed scholarship and 27 pages of bibliographic citation, Dr. Moore has gathered some of the best charts, sketches, and functional graphs from the widely scattered literature, much of it foreign (but English language). He presents us with an annotated data book of ecological patterns in the sea. With illustrations that have been little used by other summary books, the author pulls together a wealth of material on seasonal cycles, vertical zonation, vertical migration, life history functions, growth patterns, and autecological factor graphs. Any lecturer in marine ecology will receive this contribution with open arms as a source book for some of the best in marine literature.

In many universities there are courses entitled "marine ecology" in which organisms, life patterns, and the properties of their environment are taught with accompanying field trip survey. Under a teacher with great knowledge the miscellaneous facts come alive and many students develop a deep and lasting love of the environment. The very multitude of fascinating stories and the absence of overall schemes adds to the fun and mystery. It is for this kind of course that Hilary Moore's book can be used in richness. First he presents chapters on physical, chemical and biological factors. Then in two chapters he provides a short synopsis of the habitats of the sea. Five chapters follow on organisms and their spatial and temporal patterns. But, in the final paragraph of the review chapter, the author puts his finger on the weakness of his miscellaneous facts approach when he comments: "The science has in some of its aspects suffered from the overcollection of data to the point where the mass of material tends to become indigestible."

There will be other marine ecologists and those who teach ecology with an approach of principles who will find that the science has been sold short. They will not find here an introductory treatment of the general ecology of the sea. There is only the barest mention of the great generalizations of the sea such as the distribution of fertility, the workings of nutrient cycles, the flow of energy, the workings of population growth and regulation, the circulation machinery of the sea, dominant role of meteorology, the fundamentals of light penetration, the importance of blooms, buffer systems, the biological control of bottom geochemistry, the mechanisms of tides, waves, the constant ratios of the biologically active elements in production and regeneration, microorganisms, and the paleoecological record. The pretty story of overall ecology in the papers of Gordon Riley is scattered as after-comments concerning plankton and not in sufficient details to serve as a bridge into the literature. For the general workings of the marine environment, students must still go to Harvey, Riley, and Sverdrup. It is an elementary book in not attempting to present any difficult concepts, but it is an obscure book in providing so much description without organization. Every marine biologist must have this book, but few synecologists will recognize it as the heart of ecology. Everyone will welcome the chance to see one of the teaching approaches of the Miami Marine Laboratory.

H. T. Odum

Institute of Marine Science
The University of Texas
Port Aransas, Texas

[1] Moore, Hilary B. 1958. Marine ecology. New York: John Wiley & Sons; London: Chapman & Hall, Ltd. xi + 493 pp., figs. & tables. $9.50.

The Natural History of Terrestrial Arthropods Other Than Insects[1]

Relatively few professional zoologists are able to name all of the currently recognized classes of arthropods, much less the orders of arachnids. Cloudsley-Thompson has done research on most of these groups, and his personal familiarity with the subject matter gives his book life and authenticity. It is abundantly clear that patient and skillful study in the best Fabre tradition has gone into obtaining the information recorded in the eleven chapters.

The pattern of presentation is the same for all groups. Each chapter opens with a section on classification and distribution, followed by sections on general behavior, food and feeding habits, enemies, and reproduction and life cycle. The chapters end with one to two and one half pages of bibliography, divided into sections on identification and biology. The book is thus a compilation rather than a synthesis. The author intends it to be a source book for "natural history workers, upper school biology teachers, and university students." He has written at the level of his intended audience with great success, although anyone from amateur teen-ager to distinguished professor will find it both a convenient reference work and a means of entering the professional literature.

Two thirds of the text is devoted to the arachnids, each major order being the subject of a chapter, with five minor orders, mostly allied to the whip-scorpions, treated together. One each of the remaining chapters treats isopods, diplopods, and chilopods, and the pauropods and Symphyla are covered in a single chapter as "other myriapods."

The book is undeniably interesting, and the nonexpert is sure to find new facts in every chapter. Were it not for the word "ecology" in the subtitle, there would be nothing to criticize. The use of both ecology and natural history implies a distinction, and since the author makes the distinction, the reader could reasonably expect information on populations and ecological importance in the communities inhabited. This information is certainly available for a number of the groups considered, but only a few passing references to numbers are to be found. Certainly the soil mites, the isopods, and the diplopods

[1] Cloudsley-Thompson, J. L. 1958. Spiders, scorpions, centipedes and mites. The ecology and natural history of woodlice, myriapods and arachnids. London, New York, & Paris: Pergamon Press. xiv + 228 pp. xvii plates, 40 figs. $9.00.

have significant roles in the process of humification—an admittedly important step in the passage of energy through terrestrial communities.

A set of 43 photographs is located in the middle of the book. They are mostly good, but a more frequent indication of size would have been helpful. Some 40 drawings are located in appropriate places throughout the text. The book is well written and excellently edited; no errors of any kind were noted. The author and publisher are to be congratulated on producing a thoroughly interesting and useful work.

Nelston G. Hairston
Department of Zoology
University of Michigan

The Soil Zoology of a Belgian Oak Woods[1]

In the northeastern corner of Belgium, there remain a few greatly disturbed relict stands of the original hardwood forest, dominated by the sessile oak. The total area covered by all stands of *Quercus sessilis* amounts to three or four hectares, of which about half is in a single woods. From this unprepossessing starting point, Galoux has proceeded to do a most interesting study, whose implications go considerably beyond a few small stands of oaks.

The area lies on a high terrace originally deposited by the Meuse River, and the substrate is composed of quartz sands containing some boulders and small beds of clay. The soil is acid and very low in mineral content. It is not surprising to find the original vegetation classified as an edaphic climax. Human activity has altered the vegetation, so that most of the area not actually under cultivation consists of heath, which may or may not have a scattering of oaks. Reforestation has been attempted often, and stands of both pines and mixed hardwoods were planted in the early part of this century. Galoux undertook to analyze the soil fauna of the various habitats and to estimate the interactions between the soil animals, the plant cover, and the soil itself. Marginal at best, the community is unable to resist disturbance. The best soil found is classified as a podzolic brown soil, rather than as brown forest soil. The degradation of this soil and its fauna is followed in detail along the series: oak-birch, oak heath, young heath, and mature heath. The faunistic changes are all subtractions of species from the list in the oak-birch community, rather than substitutions or exchanges. Mites and collembolans do increase numerically, however, on the more degraded soils. Typical human interference involves grazing and periodic burning, and a secondary podzol develops rather rapidly under these conditions. Galoux feels that the loss of lumbricids is the major factor in soil degradation. Earthworms are apparently unable to cope with the leaves of ericaceous plants, and the function of decomposition falls to the fungi, which in turn support large populations of collembolans and mites. Litter decomposition is much slower under these conditions, with the result that there is a considerable accumulation of "mor," rather than a formation of "mull." Considering the nature of the parent material, none of this is surprising.

Of more general interest are the soil analyses done in the two major kinds of reforestation. In both cases, species that are absent from or unimportant in the climax community were introduced on degraded soils. In those cases where the plantations consist of pines, little improvement in the condition of the soil could be found. Galoux found much the same soil fauna in pine plantations 32 to 47 years old as he found in the heath communities. All represent degradations in the direction of podzolization. By contrast, in a stand of mixed hardwoods planted in 1901, a complete regeneration of the original soil has taken place, even though the principal species was the introduced American red oak, *Quercus borealis*. The study makes the point that the local climax is the most productive community available, and that the nearer reforestation comes to reproducing the original, the greater the production will be, and the better the condition of the soil. The substitution of different species with very similar adaptations does not appear to make much difference. The author clearly favors encouraging the development of brown forest soil wherever the climatic conditions will permit.

Only a government publication could be as lavish with tabular material and detailed descriptions as this work is. Indeed, it struck this reviewer as unnecessarily cluttered with tables, some of which are incomplete, repetitive, or uninformative. The text also contains much that is trite, especially the opening 65 pages on the forest community. This section looks more like a textbook than a research report. For a monograph, the literature review is incomplete, as American ecology is carried only up to Clements and Shelford's Bioecology, and at least two prominent reviews on the forest soil and its fauna are omitted.

Nelson G. Hairston
Department of Zoology
University of Michigan

[1] Galoux, A. 1953. La Chênaie sessiliflore de Haute Campine. Essai de Biosociologie. Station de Recherches de Groenendaal [Belgium], Travaux—Série A, No. 8, 235 pp., 9 plates, 45 tables. (Available on request from Station de Recherches des Eaux et Forêts, Groenendaal-Hoeilaart, Belgium.)

The Ecology of Invasions[1]

Dr. Joseph Grinnell used to say that all terrestrial species of animals everywhere came originally from somewhere else. When the subsidences and elevations of the earth's crust, coupled with the origin, evolution, and migration of animals and plants, are taken into account, and given geologic time, this seems to be entirely possible. At any rate, movements and consequent invasions of new territory must have characterized evolutionary history from the beginning. These natural movements alone would have resulted in complications enough. Add

[1] Elton, Charles S. 1958. The ecology of invasions by animals and plants. London: Methuen and Co., Ltd.; New York: John Wiley & Sons, Inc. 181 pp., 50 pls., 51 figs. $5.25.

to these the transfer (accidentally, involuntarily, or intentionally) of species from one place to another by man and we have plenty of problems, as a recent book by Charles Elton clearly points out.

Consider some recent possibilities of this movement of species by man. On March 7, 1936 there were 1462 ships at sea, 852 in port. In course of the activity of Fairchild's Office of Plant Introduction, United States Department of Agriculture, nearly 200,000 named species and varieties of plants from all over the world were brought into the United States. No record is given of airplanes in the air at any one time but in these days the number must be considerable. Remember also the potential movement of plants and animals by the tremendous military and naval intercourse made possible by modern wars and ultra-mobile contemporary armies, navies and air forces, as well as a steadily augmenting world-wide commercial and recreational travel. Nor are invasions for which man is responsible limited to the land. The Panama and Suez canals, accidental transport of marine forms in or on ships, fishing management, and the business of oyster and clam culture, are responsible for widespread and far-reaching alterations. As pointed out by Elton (chapter 2, pp. 33-49) Wallace's Realms, i.e. the old Neotropical, Nearctic, Palaearctic, Oriental, Ethiopian, and Australasian (with the Eastern Pacific suggested in this book by Elton) are breaking down.

Indeed, says Elton, we live in an explosive world (p. 15); and this book is concerned with ecological explosions, often involving enormous increase in the numbers of various kinds of living organisms, and far-reaching and sometimes tragic consequences to others. The author cites the pandemic of influenza at the end of World War I as one of these ecological explosions, one which was estimated to have killed 100 million persons. Other instances are the organism of plague, the potato fungus in Ireland, myxomatosis in Europe, England, and Australia, chestnut blight and the starling in North America, the muskrat in Europe. ". . . we are seeing one of the great historical convulsions in the world's fauna and flora," says Elton (p. 31). Nor are these phenomena of academic interest merely. Our modern agriculture is only maintainable by virtue of a colossal and costly protective organization. It is true that at least the most advanced third of the world's population are well fed, so to this extent things are working out pretty well. But world population is increasing, and in places human increase itself seems to be one of the most serious explosions of all. We go from crisis to crisis, no less in ecological management than in politics and economics. Many of the policies and decisions in these fields depend on a proper estimate of ecological conditions, an appraisal which, unfortunately, few of our statesmen are qualified to make.

Elton feels that we are faced with a life and death need, not just to find out how to eliminate unwanted species, but rather to rethink and rearrange ". . . much of the landscape . . . that has already been so much knocked about and modified by man; while at the same time preserving what we can of real wilderness containing rich natural communities." If Elton is right, and this reviewer, at least, is in hearty agreement with him, the intuitive sympathy of the general public and of many scientists with the preservation of wilderness is on the right track. It is possible that studies of wilderness areas may turn out to be vital to the successful ordering of our environment.

Elton makes a strong plea for leaving more of the ordering or "management" of nature to nature herself. Experiments, he thinks, should use the principles on which nature works, not those on which an engineer or chemist operates. For example, under our engineer's dream of agriculture hedges tend to vanish; but except for wild moors, lakes, and the sea England's 190,000 miles of hedges and road verges, with a far greater length bordering the mosaic of fields, constitute the last big remaining nature reserve in Britain.

Space is lacking to discuss Elton's pertinent comments on the archipelago of continents (p. 33); ecological prognosis for the future (p. 50 etc.); the effect of grazing animals (pp. 127 etc.); chemicals for control of insects (pp. 131 etc.); the desirability of better understanding of the complexities of competition and interference (p. 122); man's desire to shorten food chains (p. 127); the subtlety of population balance (p. 142), and many other points. This is just as well, as it is hoped the reader of this will be moved to read the book.

At the outset, Elton announced that his ideas form three streams of thought, which are permitted to flow together harmoniously through the pages of this book: (1) faunal history (2) ecology (3) conservation (p. 13). At the very end, the author suggests that, prior to changing, cutting away, draining, or spraying an area, it is vital to ask three questions: (1) What animals and plants live in it? (2) What beauty and interest may be lost? (3) What extra risk will changing it add to the accumulating instability of communities?

All responsible individuals and agencies, public or private, having to do with the land or the water and the world's supply of interesting and useful plants and animals (including man!) will find this volume suggestive and challenging.

WALTER P. TAYLOR
UNITED STATES DEPARTMENT OF THE INTERIOR, RETIRED

QUANTITATIVE PLANT ECOLOGY[1]

This is the first book to have been devoted to this section of the science of plant ecology—a section rather neglected by writers of general textbooks on the subject, and which has seen considerable development in the past decade. In the English-speaking world at least, the importance of the quantitative and statistical approach to plant ecology is coming to be more generally realized; and the need to include it in undergraduate courses and in research training is widely accepted. There is no doubt, then, that this book will find a welcome, in saving teacher and student from ploughing through a rather dispersed mass of original literature.

This book seems to have been written with an eye to the student in the final year of an Honours course in Botany at a British University, and would also be suitable reading for the graduate schools in plant ecology of many United States universities. The author assumes general understanding of the principles of descriptive plant ecology, and never goes out of his way to explain any of the

[1] Grieg-Smith, P. 1957. Quantitative plant ecology. New York: Academic Press Inc.; London: Butterworths Scientific Publications. x + 198 pp., 29 figs., 28 tables.

ecological points arising in his arguments. On the other hand, he assumes little statistical knowledge. One even feels it might have been better had he assumed more. Most students who have reached this stage have attended an elementary course on statistical methods; and so many good textbooks on this subject are now available that it would be very easy to refer the unprepared reader to one of them. Although no basic statistical concepts are explained, much elementary material is included; a detailed derivation of the formula for the Poisson series is given, and examples of the computation of t and of r are followed right through; on the other hand, elsewhere the author deviates too far in the reverse direction—for instance, in the explanation he gives of the Beta distribution (p. 177), and in his passing mention (p. 109) of Mahalanobis's useful D^2 statistic; in these cases lengthier explanations might have been welcome. One or two mathematical demonstrations (for instance, that of the dependence of generic coefficient on sample size) included in the text would be rather hard going for the average reader, and could well be relegated to an appendix.

The book begins with a consideration of the various quantitative measures likely to be used in describing vegetation, and then continues to questions of sampling, and the comparison of different areas by sampling. Random distribution and pattern in vegetation then come under discussion. Questions of association and correlation are then considered—first association between species, then association of vegetational features with environmental factors, leading up to the quantitative description and analysis of the plant community.

The author devotes a lot of attention to random distribution and deviations from it, to methods of recognizing these deviations, and to the effects of distribution on the relation between frequency and density. Surely this is now somewhat out-moded? The author admits that random distribution is quite exceptional and patchy distribution the rule. This being so, does much importance attach to tests of randomness?

The subject of pattern is much more "alive," and one feels with the author that this is a growing point of quantitative plant ecology. Dr. Grieg-Smith's account of his use of analysis of variance to study scale and intensity of pattern is of considerable interest—to myself particularly, since I was independently over the same period (1950-1952) developing and using with Mr. R. E. Winkworth a very similar method, of which very few results have yet been published. But it should be borne in mind that the features of pattern which can be displayed in this way are somewhat limited—to the mean quantitative features of patches of individual species, in fact. Other techniques will be necessary to study variation in patch size, irregular shape of patches, and—most important—the mutual patchiness of the various species occurring together. Nevertheless, Dr. Grieg-Smith's suggestions as to the changes in pattern (in his limited sense) during succession have considerable interest, and one will look forward to the results of further tests in the field.

Apart from the discussion of pattern, which is certainly one of the strong points of the book, one may mention for special approval the author's flexible use of contingency tests, and his discussion of spacing measures. But there are places in the book where one feels that a more critical approach might have been welcome—the repetition (p. 141) of the "circular argument" criticism of the Zürich-Montpellier school and the discussion of minimum area may be cited as examples.

Dr. Grieg-Smith has a queer blind spot. Throughout his book, there is no suggestion that ecology can be anything but an observational science. There is no mention of methods of experimental design and analysis, although more and more ecologists are attempting to supplement observation with experiment. And the considerations involved in ecological experimentation are not altogether the same as those for agriculture where one normally starts with a *table rase*—uniformity-trial techniques, for instance, are likely to be much more prominent. Another deficiency concerns the treatment of temporal changes—the use of permanent quadrats or repeated observations on the same stand to identify cyclical or progressive changes in the vegetation, and their relation to environmental factors. These deficiencies could well be made good when a second edition is prepared.

Less attention has perhaps been given to the special problems of applied ecology than they deserve. Foresters have devoted a great deal of work to sampling and estimation methods which might well be reflected in these pages more prominently than it is. The interesting methods for quick rough survey of range vegetation that have been developed in the United States are not mentioned. And some grassland work—notably that by the Dutch group under de Vries—deserves more attention than has been accorded it. Incidentally this Dutch work includes an interesting use of ranking methods; Dr. Grieg-Smith includes an example of ranking techniques, but one feels that these have a considerable future in ecological work and might have been worth more extended discussion.

But these minor strictures should not be taken seriously against a book which fills an important gap in ecological teaching, is well written and produced, and will undoubtedly be used extensively in the English-speaking countries in university departments of botany which take their ecology teaching seriously. One hopes that it will be used in the universities of Europe, too, where this aspect of ecology has been too long neglected.

The book is supplied with good indexes and bibliography, and an appendix contains some useful tables not easily accessible elsewhere.

David W. Goodall
C.S.I.R.O. Tobacco Research Institute
Mareeba, Qld.
Australia

Grassland in West Germany[1]

Wiesen und Weiden (Meadows and pastures) by E. Klapp deals with the management, improvement, and yields of grassland in West Germany. Grassland (Grünland) comprises permanent pastures and meadows which make up a total of about 5,600,000 ha., or 40 per cent of the usable land in the country. The area of meadow is about double that of pasture. This is non-tillable land; all tillable land is planted in crops. It takes the place of "rough-grazings" in Great Britain. West Germany lacks a reserve of tillable grassland such as Great Britain put to good use in the last World War.

The grasslands are productive, especially when one considers that they are on non-tillable land, often considered waste land. On the average 0.51 ha. will support one animal unit (55 kg. live weight). Under good management one animal unit can be carried on 0.20 ha. The chief characteristic of these grasslands is that they consist of a mixture of many perennial species, constituting a permanent community of a certain degree of uniformity provided that management continues in a similar way. Scrub and woodland soon invade if mowing or grazing is not continued. Permanent grassland resembles natural plant cover more closely than it resembles crop land such as sugar beets or grain, and the author stresses that better recognition of this is needed. Methods of management must be adapted to the nature of the grassland. The carrying over of agronomic methods used in the cultivation of field crops is not sufficient. This is being increasingly recognized in the United States as indicated by the greater use of ecological concepts and methods.

Much emphasis is laid upon the plastic nature of the grassland. The species composition, yield, and quality of the vegetation are subject to management practices, such as the regulation of soil moisture, including the depth of the water table, by drainage or irrigation; the kind and amount of fertilizer and the time or times of application; intensity and time of grazing; and the selection of species in accordance with site conditions. The flexibility under management is ascribable to the association of a large number of species in the pastures and meadows. This number includes some 15 kinds of grasses, 7 legumes, and 38 other kinds of herbs; as well as other species that may invade, or whose propagules are in the ground. The more favorable the environmental conditions, the smaller the number of species in the stand. Grazing simplifies the species composition as compared to mowing, by increasing the grass cover and reducing the number of forbs.

Wiesen und Weiden treats authoritatively and in detail all phases of the nature and management of permanent grasslands in West Germany, but makes little pretense of attempting to cover a wider geographic area. There is plenty to deal with in West Germany! Some of the sections of the book concern environmental conditions, important species and communities, soil water control, fertilizers, plowing and reseeding, weed control, diseases, and effects of management methods upon total yields and nutritive values. There are numerous tables and the illustrations are clear and meaningful. It utilizes facts and ideas contributed by numerous workers over many years, in addition to Dr. Klapp's own wide knowledge of this field. Most of the 533 references are German publications, a number from Great Britain, but only a few from the United States. Lists of common (German) and scientific names are appended.

This book is encyclopedic in coverage, but very readable. It contains much material for the ecologist, and it is indispensable for workers who study pastures, meadows, rangelands, or other grasslands. The land economist can use the book to advantage.

The 8th, revised, edition of Dr. Klapp's Taschenbuch der Gräser (Pocket book of grasses) contains vegetative and floral characteristics of grasses, keys to species based on vegetative and floral characteristics, drawings of the inflorescence and spikelet parts, detailed descriptions of growth characteristics, habitat relations, uses, etc., of each species. There are tables of phenologic data, seeding mixtures for various sites, indicator data, and indices of common and scientific names. It is a mine of information in very convenient form.

The paper-bound book by Klapp, Futterbau und Grünlandnutzung, (Forage culture and grassland use) in its 6th, revised edition, deals in a more practical way with all sorts of forage plants, including root crops, roughages, etc. The author estimates that about 52 per cent of the usable land in West Germany is used for the production of forage. The number of species involved is between 60 and 70. If wild plants are included the number reaches 700 to 800 species. Directions are given for sowing, harvesting, and utilization. Characteristics of the plants, habitat relations, and management methods are also discussed. This is also a most useful handbook.

Herbert C. Hanson
Biology Department
The Catholic University of America
Washington, D. C.

[1] Klapp, Ernst. 1956. Wiesen und Weiden. Verbesserung und Nutzung von Grünland Flächen. 3rd edn. Berlin and Hamburg: Paul Parey. vii + 519 pp., 175 figs., num. tables. DM 33.60, $9.00.

Klapp, Ernst. 1957. Taschenbuch der Gräser. Erkennung und Bestimmung, Standort und Vergesellschaftung, Bewertung und Verwendung. 8th edn. Berlin and Hamburg: Paul Parey. 220 pp., 750 figs., taxonomic keys. DM 9.80, $2.25.

Klapp, Ernst. 1957. Futterbau und Grünlandnutzung. Ein Wegweiser für die Praxis. 6th edn. Berlin and Hamburg: Paul Parey. 167 pp. 51 figs. DM. 8.40, $2.00.

Biological Implications of Plant Diseases[1]

Here is a book that lives up to its title. Its approach to plant pathology is along the line of general biological principles rather than through an enumeration and description of individual causative agents or individual diseases of plants. In it, one will find well-illustrated recent information about the genetics of plant pathogens and of host resistance. The nature, classification, and physiology

[1] Stakman, E. C. & J. George Harrar. 1957. Principles of plant pathology. New York: Ronald Press Co. xi + 581 pp., 136 figs., 19 tables. $8.00.

of the pathogens and of physiological diseases as well as the aspects of plant diseases, their spread and control is adequately covered. In a chapter called, "Plant Diseases of International Importance," selected diseases primarily of cereals, potatoes, and tropical fruits are considered. The influence of factors in the physical environment upon spore germination, vegetative growth, and reproduction of the pathogens is carefully considered. The chapter on quarantine, eradication campaigns and international plant protection is one of the best discussions anywhere of the biological and social aspects of this important area in plant pathology with which the authors have had personal experience. The illustrations are of very high quality and the extensive lists of selected references at the ends of each chapter and the appendix of important books in plant pathology are particularly valuable. This book is heartily recommended to all who want to learn about the present state of knowledge and the possible future developments in the field of plant pathology.

EMANUEL D. RUDOLPH
DEPARTMENT OF BOTANY AND BACTERIOLOGY
WELLESLEY COLLEGE

BOOKS AND MONOGRAPHS RECEIVED FOR REVIEW

Ahlstrom, Elbert H., John D. Isaacs, James R. Thrailkill, & Lewis W. Kidd. 1958. High-speed plankton sampler. U. S. Dept. of Interior, Fishery Bull. **58** (132): 187-214. $0.50.

***Balogh, János.** 1958. Lebensgemeinschaften der Landtiere. Ihre Erforschung unter besonderer Berücksichtigung der zoozönologischen Arbeitsmethoden. 2nd edn. Budapest: Verlag der ungarischen Akademie der Wissenschaften; Berlin: Akademie-Verlag. 560 pp., 125 figs., 84 tables.

Barrau, Jacques. 1958. Subsistence agriculture in Melanesia. Bernice P. Bishop Museum, Honolulu, Bull. **219**: 1-111.

***Bates, Marston & Donald Abbott.** 1958. Coral island: portrait of an atoll. New York: Charles Scribner's Sons. 254 pp., plates. $4.95.

***Benton, Allen H. & William E. Werner, Jr.** 1958. Principles of field biology and ecology. New York, Toronto, London: McGraw-Hill Book Co., Inc. vii + 341 pp., num. figs. $6.50.

Bliss, C. I. 1958. Periodic regression in biology and climatology. Connecticut Agricultural Experiment Station, New Haven, Bull. **615**: 1-55, 14 figs., 21 tables.

Brooks, John Langdon. 1957. The systematics of North American Daphnia. Connecticut Academy of Arts & Sciences Memoirs, Vol. **13**: 1-180, 61 plates. Also, New Haven: Yale University Press. $8.00.

Burton, Maurice. 1958. British mammals. London & New York: Oxford University Press. (Oxford Visual Series.) 64 pp., figs. 11s. 6d., $1.65.

***Buzzati-Traverso, A. A.** (editor) 1958. Perspectives in marine biology. (Symposium) Berkeley & Los Angeles: University of California Press. xvi + 621 pp., figs. & tables. $10.00.

***Clausen, Jens & William M. Hiesey.** 1958. Experimental studies on the nature of species. IV. Genetic structure of ecological races. Carnegie Institute of Washington Publication **615**: 1-312. 33 figs. & 68 tables. $4.25.

***Cold Spring Harbor Symposia on Quantitative Biology.** Vol XXII. Population studies: Animal ecology and demography. (Symposium) 1958. Cold Spring Harbor, N. Y.: The Biological Laboratory. xiv + 437 pp., figs. & tables. $8.00.

Conant, Roger. 1958. A field guide to reptiles and amphibians of eastern North America. Boston: Houghton Mifflin Company; Cambridge: Riverside Press. xiii + 366 pp., 61 figs., 40 color plates, 248 maps. $3.95.

***Cooper, William S.** 1958. Coastal sand dunes of Oregon and Washington. Washington, D. C.: Geological Society of America Memoir **72**: 1-169, 12 figs., 22 plates, 8 tables.

Crafts, A. S. (editor) 1958. Annual review of plant physiology, Volume 9. (Symposium) Palto Alto: Annual Reviews, Inc. vi + 510 pp., figs. & tables. $7.00.

Curry-Lindahl, Kai. 1955. Djuren och människan i svensk natur. (Animals and man in Swedish nature.) Stockholm: Lars Hökerbergs Bokförlag. 463 pp., num. figs. Sw. kr. 28.50, $5.50.

Dansereau, Pierre. 1958. A universal system for recording vegetation. Montréal: Institut Botanique de l'Université de Montréal, Contrib. **72**: 1-57, 21 figs. & 6 tables.

Darwin, Charles. 1958. The problems of world population. The Rede lecture 1958. Cambridge & New York: Cambridge University Press. 42 pp. $0.75.

***Dauvillier, A.** 1958. L'origine photochimique de la vie. Paris: Masson & Cie. (Collection Évolution des Sciences N° 11.) 214 pp., 27 figs. 1.300 fr., $3.80.

Finley, Robert B., Jr. 1958. The wood rats of Colorado: distribution and ecology. Lawrence: University of Kansas Publications, Museum of Natural History **10**(6): 213-552, 8 figs., 34 plates, 35 tables.

***Francis, Roy G.** (editor) 1958. The population ahead. (Symposium) Minneapolis: University of Minnesota Press. x + 160 pp., $3.75.

Furon, R. 1958. Causes de la répartition des êtres vivants. Paléogéographie—biogéographie dynamique. Paris: Masson & Cie (Collection Évolution des Sciences N° 10). 168 pp., 15 figs. 1.000 fr., $2.90.

Griffin, Donald R. 1958. Listening in the dark. The acoustic orientation of bats and men. New Haven: Yale University Press. xviii + 413 pp., 15 figs., 16 plates, 12 tables. $7.50.

Guilcher, André. 1958. Coastal and submarine morphology. Transl. from the French by B. W. Sparks & R. H. W. Kneese. London: Methuen & Co. Ltd.; New York: John Wiley & Sons Inc. 274 pp., 40 figs.

Hamilton, William J. 1958. Life history and economic relations of the oppossum (*Didelphis marsupialis virginiana*) in New York State. Ithaca: Cornell University Agricultural Experiment Station Memoir **354**: 1-48, 12 figs., 6 tables.

Harlow, William M. & Ellwood S. Harrar. 1958. Textbook of dendrology, covering the important forest trees of the United States and Canada. 4th edn. New York, Toronto, London: McGraw-Hill Book Co., Inc. xi + 561 pp., 236 figs. $8.75.

Hough, Jack L. 1958. Geology of the Great Lakes. Urbana: University of Illinois Press. xviii + 313 pp., 75 figs. $8.50.

Indo-Pacific Fisheries Council Proceedings. 6th Session, Tokyo, Japan, 30th September—14th October, 1955. 1957. Bangkok: Indo-Pacific Fisheries Council Secretariat, Food and Agricultural Organization of the United Nations Regional Office for Asia and the Far East. Section I, pp., 1-175; Section II & III, pp. 175-450. Figs. & tables.

Jørgensen, C. A., Th. Sørensen, & M. Westergaard. 1958. The flowering plants of Greenland. A taxonomical and cytological survey. København: Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter 9(4): 1-172, 6 tables. D.kr. 27.00, $4.00.

Macnae, William & Margaret Kalk. (editors) 1958. A natural history of Inhaca Island, Moçambique. (Symposium) Johannesburg: Witwatersrand University Press. v + 163 pp. 30 figs., 11 plates, keys & habitat lists. 2 Guineas.

Magner, Thomas F. 1958. Manual of scientific Russian. Minneapolis: Burgess Publishing Co. iii + 101 pp. $4.60.

***Neal, Ernest.** 1958. Woodland ecology. Cambridge, Mass.: Harvard University Press. xii + 117 pp., 16 figs., 8 plates, 7 tables. $1.75.

***Pierre, Franklin.** 1958. Écologie et peuplement entomologique des sables vifs du Sahara Nord-Occidental. Paris: Centre National de la Recherche Scientifique, Publications du Centre de Recherches Sahariennes, Série Biologique N° 1. 332 pp., 140 figs., 16 plates, 35 tables. 3.200 fr., $9.25.

Rasche, Herbert H. 1958. Temperature differences in Harvard Forest and their significance. Petersham, Mass.: Harvard Forest Papers 1(4): 1-153, 109 figs., tables.

Robertson, William B., Jr. 1958. Investigations of ring-necked pheasants in Illinois. Springfield: Illinois Department of Conservation, Division of Game Management, Tech. Bull. No. 1: 1-137, 27 figs., 61 tables.

Rounsefell, George A. 1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. U. S. Dept. of the Interior, Fishery Bull. 58(130): 83-169, 61 figs., 44 tables. $0.55.

Russell, Norman H. 1958. An introduction to the plant kingdom. St. Louis: C. V. Mosby Co. 353 pp., 184 figs. $5.50.

St. John, Harold. 1958. Nomenclature of plants. A text for the application by the case method of the International Code of Botanical Nomenclature. New York: Ronald Press Co. vii + 157 pp. $2.50.

Sinnott, Edmund W., L. C. Dunn, & Theodosius Dobzhansky. 1958. Principles of genetics. 5th edn. New York, Toronto, London: McGraw-Hill Book Co., Inc. xiv + 459 pp., num. figs., tables. $6.75.

Smith, Guy-Harold. (editor) 1958. Conservation of natural resources. 2nd edn. (Symposium) New York: Wiley & Sons, Inc.; London: Chapman & Hall, Ltd. xi + 474 pp., figs. & tables. $8.50.

Stanier, Roger Y., Michael Doudoroff, & Edward A. Adelberg. 1957. The microbial world. Englewood Cliffs, N. J.: Prentice-Hall, Inc. xxii + 682 pp., num. figs., tables. $8.50.

Steere, William Campbell. (editor) 1958. Fifty years of botany. Golden jubilee volume of the Botanical Society of America. (Symposium) New York, Toronto, London: McGraw-Hill Book Co., Inc. xiii + 638 pp., figs. & tables.

***Stefferud, Alfred.** (editor) 1958. Land. The yearbook of agriculture, 1958. (Symposium) Washington; U. S. Department of Agriculture. xi + 605 pp., figs. & tables. $2.25 (Superintendent of Documents, Washington 25, D. C.)

Stewart, Robert E. & Chandler S. Robbins. 1958. Birds of Maryland and the District of Columbia. U. S. Dept. of the Interior, Fish & Wildlife Service, North American Fauna No. 62: 1-401, 69 figs. $1.75 (Superintendent of Documents, Washington 25, D. C.)

Thimann, Kenneth V., William B. Critchfield, & Martin H. Zimmermann. 1958. The physiology of forest trees. (A symposium held at the Harvard Forest, April, 1957, under the auspices of the Maria Moors Cabot Foundation) New York: Ronald Press Co. xvi + 678 pp., 226 figs., 66 tables. $12.00.

Tiffany, Lewis Hanford. 1958. Algae: the grass of many waters. 2nd edn. Springfield: Charles C. Thomas. xv + 199 pp. 13 figs., 41 plates, 4 tables. $6.50.

***Tüxen, Reinhold & Erich Oberdorfer.** 1958. Die Pflanzenwelt Spaniens. Ergebnisse der 10. Internationalen Pflanzengeographischen Exkursion (IPE) durch Spanien 1953. II. Eurosibirische Phanerogam-Gesellschaften Spaniens mit Ausblicken auf die Alpine- und die Mediterran-Region dieses Landes. Veröffentlichen des Geobotanischen Institutes Rübel in Zürich 32: 1-328, 27 figs., 15 maps, 92 tables. Bern: Verlag Hans Huber. SFr/DM 38.30, $9.20.

Uggla, Evald. 1958. Ecological effects of fire on North Swedish forests. Uppsala: Almqvist & Wiksells Boktryckeri AB. 18 pp., 2 figs.

Uggla, Evald. 1958. Skogsbrandfält i Muddus Nationalpark. (Engl. summ.: Forest fire areas in Muddus National Park, northern Sweden) Acta Phytogeographica Suecica 41: 1-116, 66 figs. Uppsala: Almqvist & Wiksells Boktryckeri AB. Sw. kr. 21:—, $6.05.

***Walford, Lionel A.** 1958. Living resources of the sea. Opportunities for research and expansion. New York: Ronald Press Co., A Conservation Foundation Study. xv + 321 pp., 23 figs., tables. $6.00.

Weatherley, A. H. 1958. Tasmanian farm dams in relation to fish culture. Melbourne: Commonwealth Scientific & Industrial Research Organization, Australia, Div. of Fisheries & Oceanog. Tech. Paper No. 4: 1-24, 12 figs., 4 tables.

***Welten, M. & H. Zoller.** (editors) 1958. Festschrift Werner Lüdi. (Symposium) Veröffentlichen des Geobotanischen Institutes Rübel in Zürich 33: 1-292, figs., & tables. Bern: Verlag Hans Huber. SFr/DM 26.80, $6.40.

Wooster, Warren S. & Townsend Cromwell. 1958 An oceanographic description of the eastern tropical Pacific. Bull. Scripps Inst. of Oceanog., Univ. of Calif., La Jolla, 7(3): 169-282, 2 figs., 36 profiles. Berkeley & Los Angeles: University of California Press. $5.00.

* Assigned for review.